Aspects of the Biology of the Cool-Temperate Scorpion: *Cercophonius squama* in Tasmania

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It deserves notice that several writers,
including well-known arachnologist Walckenaer,
have declared that spiders are attracted to music.

- Darwin 1883

Female *Cercophonius squama* giving birth
8/01/02

"How vain it is to sit down to write
when you have not stood up to live"

- Thoreau

Abstract

This project investigated sexual dimorphism of the scorpion, *Cercophonius squama,* in southern Tasmania using morphometrics. Results were applied in a population investigation, which explored the density and seasonal variability of activity in a population of scorpions in Hobart, Tasmania. The reproductive behaviours were observed and recorded for the first time in this species and a predictive model of distribution for *C. squama* in Tasmania was developed.

A set of eight measurements was taken from individuals and a MANOVA was performed to test for any differences between the sexes. A capture mark and release program was employed to study the size and surface activity of the population during the summer months. Reproductive behaviours were recorded in the laboratory under low intensity red and white light. A new biogeographical regionalisation model for Tasmania was used to develop a theoretical distribution of *C. squama* in the state.

Males and females are significantly different from each other using morphometrics. Additionally, a secondary sexual characteristic was found in mature males that can identify sex in adults. Seasonal activity is different between males and females. Females have a peak in late spring, which coincides with the late stages of embryonic development. The surface activity of males increases throughout the summer to peak in autumn during the mating season. Juveniles are less abundant than adults and do not demonstrate a peak in activity during anytime of the year. Females give birth to 20-30 young during late summer to autumn in southern Tasmania. Mating occurs in

autumn, soon after birth. A naïve model was developed that needs verification with sampling of predicted areas.

This study gained valuable information about the biology of *C. squama* that can be used in future investigations. This scorpion appears to demonstrate life history strategies similar to those of other scorpions (vivipary). An environmental cline in reproduction may occur across the state with the colder, higher elevation regions lagging behind in the time of year in which females give birth. Investigations into population dynamics, geographical variation and reproductive ecology can now be undertaken with this species.

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Chapter 1

General Introduction

Scorpions are long-lived viviparous arthropods that successfully made the sea to land transition 410 million years ago (Jerum 2001). Since their terrestrial invasion, scorpions have radiated to most regions of the globe. They are found on all continents between 60° N and 60° S but diversity is very reduced at latitudes greater than 40° (Polis 1990). The greatest diversity is found in xeric environments of the subtropics. In some habitats such as deserts, they play a major role in nutrient recycling with a biomass greater than that of all other animals, except termites and ants, including vertebrates (Polis 2001). This illustrates the importance of scorpions in community ecology.

Basic research on the order Scorpiones expanded in the late 1970s to include physiology, behaviour, ecology, and evolutionary biology (Brownell and Polis 2001). Before then, investigations were dominated by taxonomy and scorpion toxicity (Brownell and Polis 2001). Consequently, scorpion biology is still in its infancy and there have been relatively few long-term investigations on these cryptic animals.

Life History

Scorpion life-history strategies are different from most arthropods. Unlike many other arthropods, scorpions do not have a separate larval stage that requires metamorphosis to an adult form (Williams 1969, Francke 1981, Hjelle 1990, Polis

and Sissom 1990, Audesirk and Audersirk 1996, Hickman *et al.* 1997). Scorpions can live up to 25 years and all have the potential to be iteroparous (Polis and Sissom 1990). The major contrast between all scorpions and other arachnids, with the exception of a few mites, is their viviparous reproductive strategy (Hickman *et al.* 1997). They can be readily observed in their environment and are easily kept in the laboratory. These characteristics predispose them to be used as models for answering fundamental questions such as parental investment and reproductive output.

Australian Scorpions

Three families of extant scorpions are found in Australia with two endemic genera (Table 1.1). The genera *Urodacus* and *Isometroides* are endemic to Australia with 19 and 1 species respectively. *Cercophonius* was considered endemic to Australia until 1996, when a new species was discovered from the Himalayas of India (Lowe and Fet 2000).

Table 1.1 Scorpion family and genus diversity in Australia

Family	Family Distribution	Genus	# of sp. in Australia
Bothriuridae	S. America, S. Africa, India & Australia	*Cercophonius*	6
Buthidae	Cosmopolitan	*Lychas*	3
		Isometroides	1 (Endemic Genus)
		Isometrus	2
Scorpionidae	Africa, Asia & Australia	*Liocheles*	3
		Urodacus	19 (Endemic Genus)

Source: Koch 1977 and Fet *et al.* 2000

Biogeography of the bothriurids

Cercophonius is the only genus of the Bothriuridae family in Australia, which is the only scorpion family with a Gondwana distribution (Sissom 1990, Lowe and Fet 2000). The centre of bothriurid diversity is South America, with *Cercophonius* from Australia, and *Lisposoma* from Africa, being the only genera occurring outside South America (Fig. 1.1) (Lowe and Fet 2000). They have close affinities to the South American bothriurids and cannot be separated morphologically into a separate subfamily (Lowe and Fet 2000). Their Gondwana distribution implies that they are an ancient group.

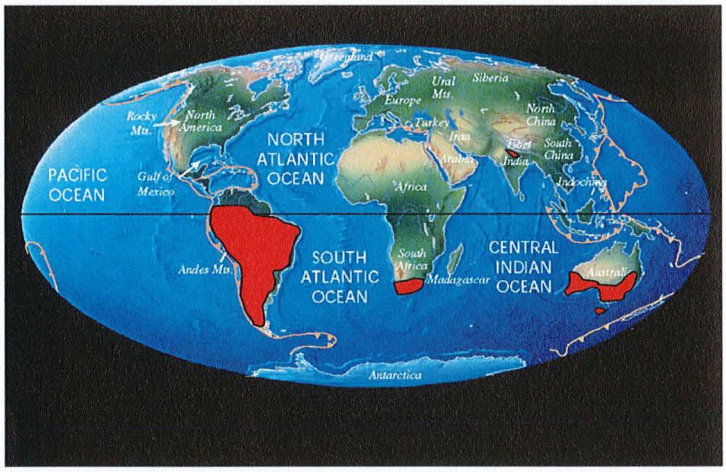

Figure 1.1 Areas in red show the geographical distribution of the scorpion family Bothriuridae.

Biogeography in Australia

The distribution of *Cercophonius* is near the environmental limits of known scorpion distribution and thus makes a good model for comparison with other genera. *Cercophonius* spp. are found in Australia across a broad geographical range from wet sclerophyll forest in Tasmania, to dry regions in Victoria and Western Australia

(Koch 1977, Acosta 1990, Lowe and Fet 2000). This lends itself to be used in biogeographical investigations. Furthermore, a recently described species from the Himalayas, *Cercophonius himalayensis* (Lowe and Fet 2000), may be the link between the South American and Australian bothriurids. This is a disjunct distribution very distant from the other species of *Cercophonius,* exclusively found in Australia, and may help to explain and clarify the radiation of the genus in Australia.

Koch (1977) listed two possible explanations for the evolutionary radiation of *Cercophonius* in Australia:

(1) a widespread connection across northern areas followed by northern extinction: and

(2) a connection across a previously continuous southern land mass.

Koch (1977) concluded that the second hypothesis best explained the current distribution. Australia moved northwards in the geologic past; warming and drying the northern areas, which probably caused local extinction and restricted *Cercophonius* to the cooler, moister regions. The Indian subcontinent experienced a similar change when it became hot and dry in the south, and this could have restricted *C. himalayensis* to cooler, wetter regions in the north. The absence of *Cercophonius* from New Guinea supports the idea that its distribution is a true Gondwana distribution. Further investigation of the biogeography and ecology of the species will help to determine the processes that have shaped its distribution.

Biogeography in Tasmania

Cercophonius is the only scorpion genus in Tasmania and is represented by a single species, *C. squama*. *Cercophonius squama* has the largest geographical range in the genus and has the most southerly extent (Acosta 1990). It is unusual by inhabiting wet temperate forest to latitudes above 40°. Ecogeographical adaptations have been well studied in endothermic vertebrates, as illustrated by the generalisations of Bergman's rule, Gloger's rule and Rapoport's rule (Strickberger 1996), but far fewer studies have focused on the more numerous invertebrates. Hence, the factors determining the geographical relationships of many invertebrates are not well known (Darlington 1957).

Future investigations of scorpions will deliver insight into questions of reproductive strategies such as parental investment in embryonic development, mate location, geographic variation and many more. This study is a preliminary investigation into the biology of *Cercophonius squama* in Tasmania, to provide a base knowledge for future ecological studies.

The specific aims were to:

1) distinguish sexual dimorphism using morphometrics;
2) determine the density of a population in southeastern Tasmania;
3) determine temporal variation in activity;
4) investigate reproductive biology; and
5) determine the geographical distribution of *C. squama* in Tasmania.

Chapter 2

General Methods

2.1 Study Site

Tasmania provides a strong contrast to studies of scorpions undertaken in arid environments in the Northern Hemisphere. Tasmania is an island state located off the southeast tip of the Australian mainland between 39 and 43° South latitude and between 143 and 149° East longitude. Tasmania is separated from the Australian mainland by Bass Strait, which at its narrowest is about 240 km wide. With its smaller islands, it occupies a total area of 55,000 km^2. The climate is temperate maritime with mild winters and cool summers.

The study site chosen for the population study was located near the University of Tasmania, lying approximately 3 km south of the central business district of Hobart in southeastern Tasmania. It is located at the base of Mount Wellington and on the shores of the Derwent Estuary. Specimens for the recapture program were collected from a 190 m long by 2 m wide section of path in Hytten Gully, located 50 m a.s.l. (Fig. 2.1).

Figure 2.1 Lower Hytten Gully, Sandy Bay, Tasmania: population ecology study site.

No information was available on the distribution or microhabitat of *C. squama*, so site selection was arbitrary until confirmation that scorpions could be found in the area. This site was chosen for the study because it was easily accessible by a walking track that enabled collection at night without a high risk of injury and preliminary investigations established that scorpions inhabited the gully. Its proximity to the University afforded numerous collections and observations.

The gully is characterized as wet sclerophyll forest, about 20 m tall, dominated by *Eucalyptus globulus* over an understorey of *Dodonaea viscosa*, *Bergeria viscose*, *Acacia dealbata*, *Banksia marginata*, *Bedfordia salicina* and *Pomaderris apetala* (G. Norman, University of Tasmania, pers. comm.). The site shows a slight gradient down slope, with more typical wet sclerophyll species, *Bedfordia salicina* and *Pomaderris apetala* dominating at the lower end. Occasional woody weed species are present, represented by *Cotoneasta* sp. These weed species are presumably related to nearby disturbances and the closeness of developed areas. The site occurs on

dolerite with skeletal soils. The soil is mostly covered with bark and leaf debris up to 15 cm thick.

Two additional sites were used for collecting specimens needed for dissection and laboratory trials. Site 1 was Lambert Park, located 1 km south of Hytten Gully at approximately the same elevation (Fig. 2.2). This site was chosen because of its location and similarity to microhabitats of the other sites. Site 2 was the upper part of Hytten Gully, 100-150 m a.s.l. (Fig 2.3). A road barrier divides the upper and lower parts of Hytten Gully. This site was chosen because of location and the availability of scorpions. More sites around Tasmania were not established because of the cost of travel and the impracticality of sampling these sites many times.

Figure 2.2 Lambert Park, Sandy Bay, Tasmania: scorpion collection site.

Figure 2.3 Upper Hytten Gully, Sandy Bay, Tasmania: scorpion collection site.

2.2 Scorpion Collecting and Handling

Since scorpions are nocturnal, all fieldwork was done at night. The cuticle of all scorpions fluoresces under near ultraviolet light (300-400 nm) and exploiting this property allowed easy observation and collection. A torch was specially designed to achieve the correct wavelength, appropriate size and durability for collection.

Several trips to light shops with scorpions were needed in order to locate a light that would make them fluoresce. Finally, a fluorescent light (Sunbe-Lite 240v 26w) that made the scorpions fluoresce was found that could be used during sampling. This light had to be powered by AC electricity so an inverter had to be wired into the light. The bulb and inverter then needed to be transformed into a torch. This was achieved with a metal bar to which the light, inverter and an aluminium funnel to direct the light were attached (Fig. 2.4). The torch was powered by Powerblock 12120 (12V12Ah) directed through the inverter and into the light.

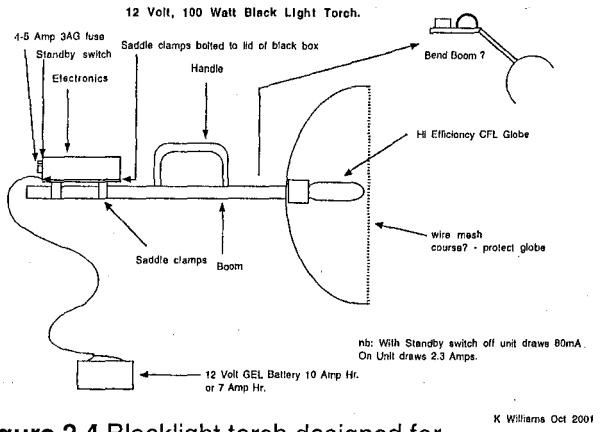

Figure 2.4 Blacklight torch designed for scorpion collecting.

Collection was generally initiated 1-2 h after sunset and finished by 01.00. Specimens were collected when their cuticle fluoresced under the torch at night. Data for the recapture program were collected over 18 nights during the 5-month period from Hytten Gully. Collections and observations occurred over additional nights in the other study sites to obtain individuals for laboratory observation, comparison and dissection.

A small pair of forceps was used to grasp the scorpions by the fourth or fifth metasomal segment. This is the hardest part of the scorpion body and reduces the risk of any injury to the animal. This technique also prevents the scorpion from stinging the collector or getting free. Once animals were captured, they were placed in individual small 75 mm x 100 mm plastic ziplock bags. Care was still needed because scorpions were able to sting through the bag. After collection scorpions were transferred to the laboratory.

Collections were aborted on nights with steady rainfall due to the risk of electric shock. The torch was designed to be water resistant and was used during drizzle and mist but steady rainfall was avoided.

2.3 Laboratory Methods

Individuals in the laboratory were housed in plastic containers 17 cm long, 12 cm wide and 6 cm deep containing a layer of soil a few centimetres deep with sufficient bark and rocks for cover. Each housing had a lid with holes in it to allow air circulation. During housing, specimens were kept at ambient temperature. Mealworms were fed to the housed individuals on a weekly basis and water was available *ad libitum.*

A set of eight measurements was taken from all captured specimens: carapace length, carapace width, fourth metasomal segment, fifth metasomal segment, length of manus, length of movable finger, length of manus with fixed finger and width of manus (Fig. 2.5). The set was adapted from, and in accordance with Acosta (1990) and Koch (1977). These measurements are typical of scorpion measuring and give a set of measurements that are consistent and comparable to other species. Carapace length is considered the measurement from the posterior edge to the anterior edge of the carapace along the medial line. Carapace width was taken at the base or posterior edge of the carapace. The fourth and fifth metasomal segment measurements were taken on the ventral side of the segment along its medial section. The length of manus was taken along the ventral side of the chela manus of the right pedipalp from the base of the movable finger. The length of the movable finger was taken along the ventral side of the right chela from the base to the tip. The length of the manus with the fixed finger was taken along the dorsal side of the right chela manus of the pedipalp from the base of the manus to the tip of the fixed finger. The width of manus was taken laterally across the manus at the widest point.

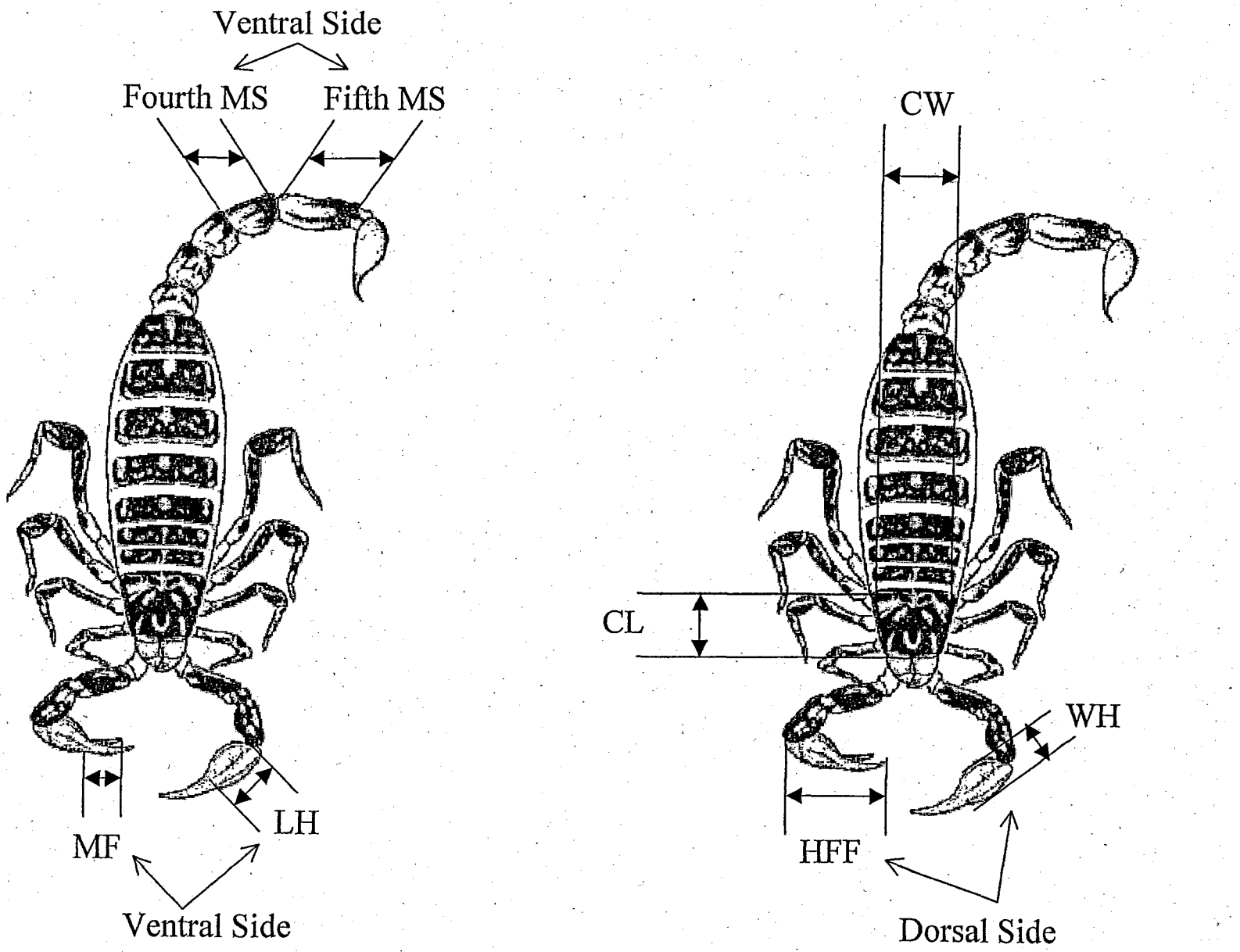

Fig 2.5 Measurements taken from *Cercophonius squama:* HFF=Manus & Fixed Finger, WH=Width of Manus, FourthMS= 4th metasoma segment, FifthMS=5th metasoma segment, MF=Movable Finger, LH=Manus, CL=Carapace Length, CW=Carapace Width

Pectinal teeth were counted during the laboratory examination of the specimens. The teeth are easily seen and counted when viewed through a dissecting scope. Teeth occur on both sides of an individual. The teeth of the right side were used during analysis unless there had been mutilation of the teeth, where counts of the left teeth were used.

Chapter 3

Gender Identification

3.1 Introduction

Determining the sex of an organism is essential if questions concerning life history or population structure are to be addressed. Sex can be determined in many animals through non-invasive investigation of sexually dimorphic features. Sexual dimorphism is common in many animals and has been related to factors such as competition for mating partners (Darwin, 1875).

Most scorpion species exhibit some sexual dimorphism in size, with the female often being the larger sex. Many scorpions also have exaggerated morphological features that separate the genders and are often associated with courtship and mating. These features are typically the pedipalps and the last two segments of the metasoma. In extreme cases, one sex can have features twice the size of the other sex. For example, *Tityus* spp. in the family Buthidae from South America demonstrate extreme elongation of the pedipalps (Polis & Sissom 1990). The scorpionid genus *Urodacus* from Australia demonstrate exaggerated elongation of the metasoma (Koch 1977). However, in *Cercophonius* spp., the only recorded dimorphism is the number of teeth on the pectine organs. Males typically have more teeth than females.

In the taxonomic key of Acosta (1990), males and females of *C. squama* are distinguished by the number of their pectinal teeth. This character is commonly used to sex scorpions (Hjelle 1972; Williams 1972; Koch 1977; Acosta 1990). Sexing by

the number of pectinal teeth in *Cercophonius squama* is, however, unreliable. Males have 15 to 20 teeth per pectine and females can have 13 to 17 teeth per pectine. Difficulties arise when trying to determine the gender of some of the specimens because individuals with 15 to 17 teeth cannot be sexed on the basis of their pectinal teeth. Animals with 15 to 17 teeth account for approximately 40% of the population.

This created a problem for any population data that were to be collected. A capture mark recapture program was planned to acquire data needed for other areas of this study. This was not feasible if the only way of sexing individuals with 15 to 17 pectinal teeth was internal exploration of the reproductive structures by dissection. An alternative way to sex individuals was therefore needed before an investigation into population structure of *Cercophonius squama* was possible.

The aim of this part of the study was consequently to find a way of determining sex in the population without sacrificing them for internal examination. Two objectives were encompassed within this aim:

(1) to try to identify a single morphological structure that would separate males from females in the field and laboratory; and

(2) to derive a reliable discriminant function for assigning sex to individuals, using a set of eight measurements.

3.2 Methods

Scorpions were collected from the study sites as described in Section 2.2 and measured as described in Section 2.3. The SPSS program (version 10.0) was used for statistical analysis.

Homogeneity of variances was tested by visual inspection of plots of group standard deviations versus group means. Normality of data was addressed by visual inspection of normal Q-Q plots and detrended normal Q-Q plots. Data were determined to be robust by meeting the requirements of normality as described by Tabachnick and Fidell (1996) and Sokal and Rohlf (1981).

The set of eight measurements (Section 2.3) from 141 animals, of known sex, was subjected to a MANOVA to identify morphometric separations between the sexes. To compensate for size, all measurements were standardised by dividing by the carapace length. Standardised measurements were used to perform a discriminant function analysis that could be used to classify individuals of unknown sex. A case wise listing of the classification was used to identify the misclassified individuals to check for error.

Along with the standard measurements taken, a detailed morphological examination of each scorpion was conducted through a dissecting microscope. The examination was focused specifically on identifying morphological characters that could distinguish between males and females in the population. The mesosomal region of 30 mature animals of unknown sex was dissected to expose the reproductive

structures. A small slit between the third and fifth segment on the right side of the mesosoma was normally sufficient to see the reproductive structures through a dissecting microscope.

3.3 Results and Discussion

After extensive examination of over a hundred specimens, a morphological feature on some of the animals became apparent. A proportion of the population exhibited a cusp or apophysis on the inside of the manus of the pedipalp. This cusp was obvious when viewed under a microscope and occurred near the base of the movable finger (Figure 3.1). This feature has not been mentioned in the literature on *Cercophonius*

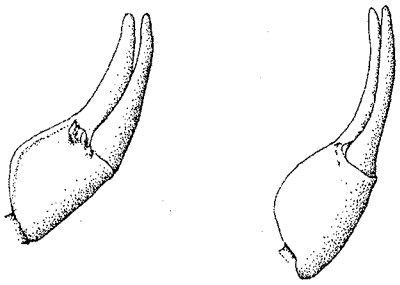

Figure 3.1 Male (left) and female (right) pedipalps of *Cercophonius squama*, showing the cusp on the inside of the male manus.

spp. Some of the known males (by the number of pectinal teeth) had this cusp, suggesting that it might present a difference between the sexes. Additionally, all individuals with a cusp on the pedipalp had a carapace length greater than 2.9 mm, suggesting that the cusp is a secondary sexual characteristic. Animals needed to be dissected to test the reliability of the cusp in distinguishing the sexes, but a minimum size had to be established to ensure maturity and any associated secondary

morphological characters. The minimum size was considered to be a carapace length of 3.2 mm because known males always exhibited a cusp at this size.

All 12 mature animals that were determined to be females by dissection lacked the cusp, while all 18 mature males possessed the cusp. The presence of this character signifies a mature male and hence all mature individuals lacking the character are females. Therefore, the cusp or apophysis is a totally reliable way of determining gender in mature animals. The cusp was never observed in animals with a carapace length of less than 2.9 mm and thus, another way of determining sex had to be found for immature individuals.

An initial MANOVA revealed carapace length was responsible for the majority of the variation between the sexes. Females were usually larger than males, but this would not help to distinguish between the sexes in smaller juveniles. Shape in *C. squama* apparently remains constant throughout life, and there is no allometric variation between juveniles and adults. For example, carapace length/carapace width is 0.73 in juveniles and 0.74 in adults. Other characters showed similar consistency. Therefore, data were standardised by carapace length to investigate relative difference between characters.

The MANOVA showed there were significant morphometric differences between the sexes. Length of manus (LH), manus and fixed finger (HFF), width of manus (WH), fourth metasomal segment (Fourth) and fifth metasomal segment (Fifth) were all found to be significantly different between males and females ($p < 0.001$). Movable finger (MF) ($F_{1,139}$=1.968, P=0.163) and carapace width (CW) ($F_{1,139}$ = .082,

P=0.775) were the only measurements not to be found significantly different in the sexes (Table 3.1).

Table 3.1 MANOVA tests of equality of group means between the sexes of *Cercophonius squama* (CW - carapace width, LH – length of manus,HFF – manus and fixed finger, MF – movable finger, WH – width of manus, Fourth – fourth metasomal segment, Fifth – fifth metasomal segment).

	Wilks' Lambda	F	df	Sig.
CW	.999	.082	1,139	.775
LH	.891	17.046	1,139	.000
HFF	.772	41.016	1,139	.000
MF	.986	1.968	1,139	.163
WH	.768	41.883	1,139	.000
FOURTH	.810	32.710	1,139	.000
FIFTH	.769	41.853	1,139	.000

After the MANOVA revealed significant differences between the sexes, a discriminant function analysis was performed to test the reliability of the characters chosen. The discriminant function formed using the five significant measurements could correctly assign sex 79% of the time. The function accounted for all of the variance using only the manus and fixed finger (HFF), the width of the manus (WH), and the fifth metasomal segment (Fifth) as coefficients. Another discriminant function analysis was performed with carapace width (CW), to see if a stronger discriminant function could be achieved. The resulting discriminant function was stronger with individuals being correctly classified 84% of the time (Table 3.2). The function used the three previous coefficients plus the fourth metasomal segment (fourth) and carapace width (CW) to account for all of the variance between the sexes (Table 3.3).

Table 3.3 Male and female classification in *Cercophonius squama* using discriminant function analysis.

Sex		Predicted Group Membership Male	Female	Total
Original Grouping	Male	82	17	99
	Female	5	37	42
%	Male	82.8	17.2	100.00
	Female	11.9	88.1	100.00

84.4% of original cases correctly classified.

Table 3.4 Standardized canonical discriminant function coefficients used in *Cercophonius squama* (HFF – manus and fixed finger, WH – width of manus, Fourth – fourth metasomal segment, Fifth – fifth metasomal segment, CW - carapace width).

	Function 1
HFF	.354
WH	.568
FOURTH	.321
FIFTH	.359
CW	-.411

This function will be very useful in investigating the population structure of *Cercophonius squama*. For the purpose of this study, the discriminant function can be applied to unknown juveniles in addition to the unknown adults that were released before the cusp was identified as a secondary sexual characteristic. The function of the cusp is unknown but it is reasonable to believe that it gives the males an advantage during the pedipalp-to-pedipalp interactions with the female (Ch. 5). *Cercophonius squama* inhabits a complex environment of leaf and bark debris, several centimetres deep. Finding a mate in this environment is likely to be uncertain and the cusp may help to increase the mating success of the male once he has located a female, for example, by helping him secure the female during mating. Cusps similar to the one seen in this species have only been recorded in the Bothriuridae family (Polis and Sissom 1990).

Chapter 4

Population Ecology

4.1 Introduction

Ecological studies involving scorpions have been limited to relatively few species. Most investigations have taken place in xeric environments of the Northern Hemisphere. The most comprehensively studied species is *Smeringurus mesaensis* of North America, which has contributed to much of the overall understanding of scorpion biology. The information on this species is very helpful but limited by its geography. In many other species, investigations have been focused on only a few ecological parameters, e.g. the role of feedback loops in the circadian system of *Androctonus australis* (Friesen *et al.* 2001) and toxicology (Housset *et al.* 1994). The limited information available for the majority of species has left large gaps in our understanding of the ecology and biogeography of scorpions.

There have been few investigations into the ecology of *C. squama.* Past studies have focused on taxonomy (Koch 1977, Acosta 1990 & Fet *et al.* 2000). Margules *et al.* (1994) explored the effects of habitat fragmentation using island biogeography theory with *Cercophonius squama.* Smith (1983) recorded the species from Ayers Rock and postulated that the springs may support a relict population of this usually wet adapted species. The species is geographically important and knowledge of its ecology would be valuable. With *Paruroctonus boreus*, which occurs in the pacific-northwest of North America (Sissom 2000), *C. squama* in Tasmania is unusual in inhabiting cool-temperate forest with often high rainfall. This lends itself to a whole suite of

ecological comparisons with species already studied, most of which occur in arid environments. The wide range of *Cercophonius squama* also invites intra-specific studies.

The aim of this part of the project was to gather information on population size, and activity so that fundamental questions could be answered in the future.

4.2 Methods

Collections were temporally random throughout each month to achieve a representative sample of the population over different moon phases. Collection methods were as described in Chapter 2.2. Captured individuals from the study site were measured as described in Chapter 2.4, sexed as described in Chapter 3, and marked before returning them to the environment. Wooden stick markers with fluorescent tape around the top marked the locations of captures. The date and number of the scorpion was written on the marker so that they could be returned to the same location and the movement of future captures could be tracked with these markers.

Collection of animals was carried out over a 5-month period from November to March. Individuals were collected and marked with pink nail polish that was applied with a pair of fine forceps. A marking system similar to a bar code system was developed and applied to the population so that each individual could be marked uniquely. This was achieved by separating each tergite of the mesosomal segment into three sections. The left third of the dorsal tergite represented the number 1, the

4.1). When this was applied to all seven segments of the mesosomal region, 2186 individual marks could be achieved (**EX:** $[(3)^7 - 1] = 2186$) (Figure4.1). The numbering started with the seventh tergite and progressed through to the first. Figure 4.2 shows an example of a marked animal. An alternative equation was also developed if more than 2186 individuals needed to be marked or if specific information for scorpions needed to be designated. This alternative method created almost an infinite number of markings by using different colours (M. L. Bush pers. comm.). Individual colours could be used to designate different locations, gender or week captured.

Alternative marking equation:

If more than one colour was used for markings;

$$C=(x+1)^n-1$$

x = # of colours; n = # of tag sites on individual

EX: $C = (5 + 1)^{21} - 1$; $C = 2.193695064^{16}$

Figure 4.1 A marked scorpion for the mark-recapture study. This individual is marked with the number 0002300.

Cuticle marking, similar to that employed for this study, has been successful in North America to mark scorpions (Hadley & Williams 1968, Polis & Farley 1980). Laboratory animals were marked and observed to test whether any adverse affects were apparent. These animals demonstrated no abnormal behaviour. The marking did not affect their food acquisition or physical survival. During the study, marked laboratory animals were kept in housing that mimicked the natural environment to test the longevity of the marks. Marks persisted on the individuals for the length of the study with little if any wear.

The Jolly-Seber method (Seber 1986, Pollock *et al.* 1990) was to be used to estimate population size because mortality, natality and migration are estimated parameters in this method. At the end of the capture, mark and recapture program an attempt was made at estimating the population size by removing individuals and calculating the change in ratio.

The number of collected individuals for each month was divided by the number of sampling efforts for that month. This yielded the mean number of captures for each month, and gave comparable numbers for between month comparisons.

4.3 Results

4.3.1 Population Size

Only two marked individuals were recaptured during the study period. The first individual was recaptured 20 days after its original capture and the second was

recaptured 43 days after its original capture. Mean surface density was spatially variable with up to 6 adults found in a 3-metre section of the path or none found for several metres. Mean surface density per night was 0.024 scorpions per m_ in November, 0.023 per m_ in December, 0.021 per m_ in January, 0.060 per m_ in February and 0.068 per m_ in March. This gave an average density during the study season of 0.039 scorpions per m^2 every night or 1 scorpion for every 26 m^2.

One hundred and twenty eight animals were removed in five consecutive days and kept in the laboratory. The number collected in successive nights showed no sign of a decrease; therefore, a population estimation could not be made. Eighteen scorpions were collected the first night, followed by 22 the second, 36 the third, 22 the fourth, and 30 the last night.

4.3.2 Seasonal Activity

A total of 242 individuals were captured, marked and released during the months from November to March. In November 42 specimens were captured, 30 in December and January, 52 in February and 88 in March (Fig. 4.2). During the month prior to sampling the study population, females appeared to have a relative abundance similar to that recorded for November. There are no quantitative data for this period because the capture release program had not begun and individuals were collected from an adjacent site.

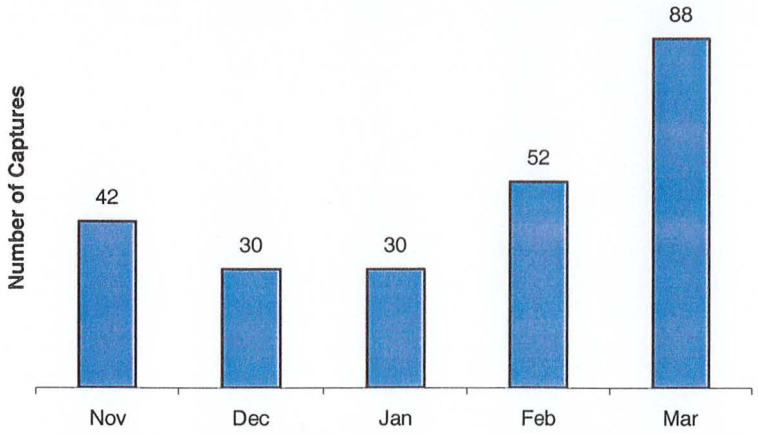

Figure 4.2 Total monthly captures, i.e. not corrected for sampling effort of *Cercophonius squama* from November to March along a 190 m path in Hytten Gully, Tasmania.

Males and females demonstrate different activity patterns during the summer. Total female and male captures were: 35 and 7 in November, 10 and 20 in December, 12 and 18 in January, 19 and 33 in February, and 22 and 66 respectively in March. Mean capture rates reveal that females display a single peak in activity during November while males exhibit a steady increase as time progresses (Fig. 4.3).

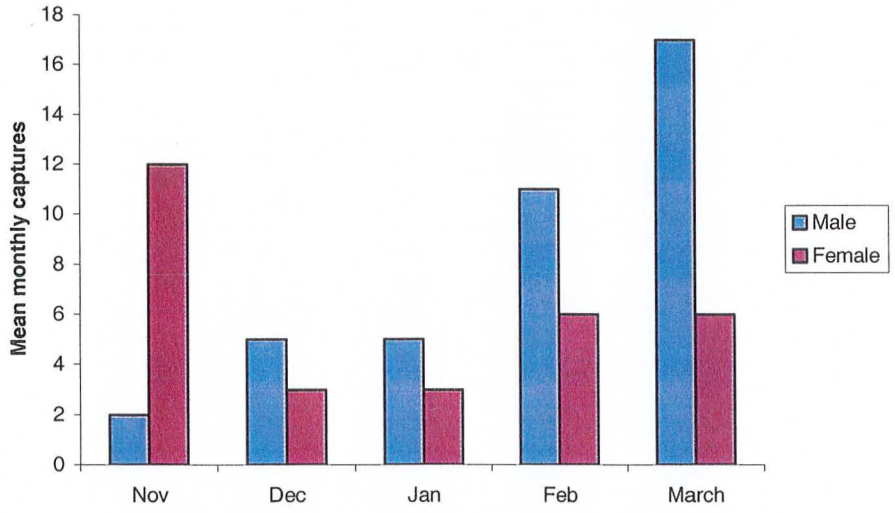

Figure 4.3 Mean sex specific captures rates, corrected for sampling effort, of *Cercophonius squama* along a 190 m path of Hytten Gully, Tasmania.

Juvenile scorpions, carapace length < 3.1 mm, made up 35% of the population captured during the study period. They express different activity patterns from males and females (Fig. 4.4). November was the least active month for juveniles with an average of only 1 capture per night. In December this increased to 2.5 a night, January decreased slightly to a mean of 2.25, February increased with a mean of 5.6 and the average in March decreased to 4 individuals a night.

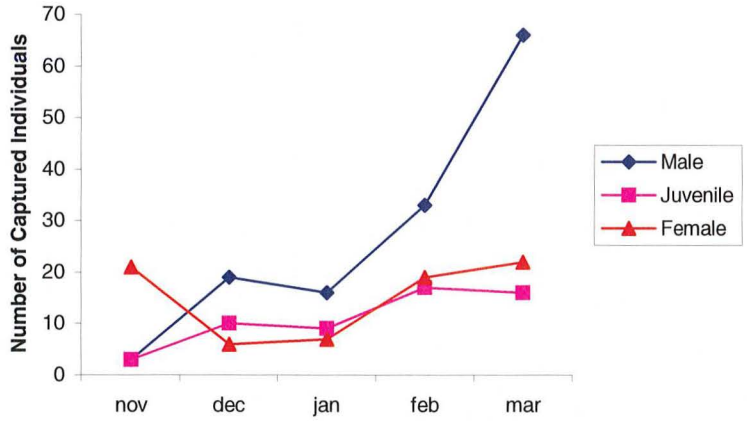

Figure 4.4 Total size and sex specific monthly captures of *Cercophonius squama* from November to March along a 190 m path in Hytten Gully, Tasmania.

Surface activity varied temporally throughout the night. Scorpions became active approximately 30-60 minutes after sunset. They remained active for approximately two hours, and then gradually became less active as the night went on (*personal observation).*

4.4 Discussion

4.4.1 Population Size

Population size could not be estimated because the Jolly method relies on multiple recaptures to estimate the size of a population (Blower *et al.* 1981, Seber 1986,

number of individuals captured during successive collections (Blower *et al.* 1981 & Seber 1986).

The path was not an ideal site for collecting because of the large edge affect. Attempts were made to sample off the path, but walking at night with the torch proved to be risky in this environment. There was an edge affect but scorpions are not considered to be highly mobile animals (Hadley & Williams 1968, Polis & Farley 1980, Bradley 1988, Polis 1980) and numerous recaptures were expected. The only time of year scorpions appeared to be on the move was in autumn, during the mating season.

A stream bordered the path 10 m to the right and a road bordered 10 m to the left. The road also blocked one end of the gully and the path crossed the other end. Scorpions cannot swim so migration across the stream is unlikely. The only feasible migration route would be along the gully between the road and stream. Scorpions using this route would probably be captured as they crossed the path if they were migrating. The limited recaptures and the removal technique suggest there is a large population in the gully.

A population estimate was not achieved but surface density will be useful for intraspecific comparisons with other locations to derive more or less suitable habitats. Surface densities can be used to compare abundance to other species of scorpions. Polis and McCormick (1986) found densities of four scorpion species in a community to range from 0.0005 per m^2 (*Paruroctonus luteolus*) to 0.77 per m^2 (*Smeringurus mesaensis*). The density of *Cercophonius squama,* 0.039 per m^2, is greater than three

mesaensis). The density of *Cercophonius squama,* 0.039 per m^2, is greater than three of the four species surveyed by Polis and McCormick (1986) but substantially lower than they found in the dominant species, *Smeringurus mesaensis*. The capture rate is probably less for *Cercophonius squama*; fewer individuals would be seen in the complex leaf litter debris that it inhabits than in the relatively open sand dune habitat that *Smeringurus mesaensis* inhabits (Polis & Farley 1980).

It may be possible that the lack of multiple recaptures for *C. squama* is due to a low surface activity coupled with low capture rates created by the complex habitat. Only a small proportion of the population may be active on the surface at one time, e.g. in *Paruroctonus utahensis*, only 3-5% of the population is active during a single night (Bradley 1988). Polis (1980) found *Smeringurus mesaensis* were active on fewer than 40% of all nights. If *Cercophonius squama* has a low surface occurrence like *P. utahensis*, 20 consecutive nights would be needed to capture all animals in the population. If a conservative estimate of 5% was applied to *C. squama* based on the surface activity of *P. utahensis,* the population could be calculated to have approximately 280 individuals based on the average capture rates during the study period. This is probably an underestimate because 128 were collected after the 242 were marked and none of these were marked. Adults do not molt and marks have persisted in the laboratory as well as the field. Marks on juveniles could have been lost during molting, but only 35% of the marked individuals would be in this category. Migration could have created few recaptures but the study site is essentially closed. Scorpions are probably very abundant in the area and a more intense study, using multiple techniques will be needed to determine the population size.

4.4.2 Seasonal Activity

Surface activity patterns change through the summer. Two peak periods were seen during the sample season, one for females in late spring and a second in early autumn. *Paruroctonus utahensis* from North America demonstrates a similar seasonal variation with less surface activity occurring in July and August (Bradley 1988).

Looking at the surface activity of the sexes separately helps our understanding of the life cycle of *Cercophonius squama*. Males and females demonstrate very different activity patterns. Male activity increases steadily over summer to peak in autumn, which coincides with the mating season (Ch. 5). Females are most active in the spring coinciding with the late stages of embryonic development (Ch. 5). Presumably, late stage embryos impose their maximum energy demand on the female at this time. This probably necessitates the increased foraging activity. Female activity declines in January, which is the birthing season for *Cercophonius squama* around Hobart (Ch. 5). Females go into seclusion prior to birth, through to the brooding of the first instars explaining the low surface activity of females seen during mid summer (pers. obs.).

Juveniles demonstrate an intermediate pattern with a general increase from November to February, then a slight decrease in activity in March. Surface activity is less in juveniles, suggesting that they are either less active on the surface or they are fewer in number. Smaller size classes often exploit different niches than adults (Polis and McCormick 1986 & Wissinger 1992) and the juveniles may stay in the leaf litter where they are not seen as often as the adults. Scorpions demonstrate a high mortality

rate in the early stages of life (Smith 1966 & Polis 1980) and the surface activity of *C. squama* may correctly reflect a population structure consisting of only 35% juveniles. However, it is suspected that the smallest size classes occupy a different niche than the adults and are captured less, because 85% of the active juveniles had a carapace length of 2.9-3.1 mm suggesting that only 15% of the active population were young juveniles. If this were representative of the population, it would appear to be a shrinking population (Audersirk 1996). Clearly, further investigations are needed to ascertain the dynamics of the population.

Records reviewed at the Tasmanian Museum and Art Gallery revealed that there is no activity during July and only very limited activity in the other winter months. The results for this study are only from the Hobart area and future investigations should incorporate different localities. The Central Highlands are believed to have a different pattern due to the variation in climate (Ch. 5).

Chapter 5

Reproduction

5.1 Introduction

5.1.2 Mating

Scorpions are solitary animals that avoid each other to reduce the risk of cannibalism (Polis 1981). In encounters, the larger individual is normally the survivor of the confrontation. This creates problems for males and females during the mating season. Males are the more active of the two sexes and go in search of females. The male's pectines act as chemoreceptors that recognise pheromones left behind by females, enabling him to follow and locate potential females (Gaffin & Brownell 2001). Once the male locates the female he is in serious risk of death because the female is usually the larger sex.

Another problem scorpions face in reproduction is the initial transfer of sperm from male to female. Sperm transfer is indirect, with the male depositing his spermatophore on the substrate while directing the gonopore of the female over it (Polis 1990). It is unlikely that the female would find and be able to take up the spermatophore without the help of the male.

To decrease the risk of death and ensure sperm transfer, scorpions have developed a complex array of courtship behaviours. Scorpions demonstrate a sequential

progression of characteristic behaviours throughout the mating process that facilitates mate recognition and spermatophore uptake by the female (Benton 2001).

5.1.2 Parturition

It was once believed that three forms of reproduction were expressed by scorpions; vivipary, ovovivipary, and ovipary (Williams 1969). We now know that all scorpions are truly viviparous but can be separated by the nature of embryonic development (Francke 1982). Oocytes in apoikogenic development occur in association with the ovariuterus, while the oocytes in katoikogenic development occur in specialized diverticula that branch off of the ovariuterus (Polis & Sissom 1990). The family Bothriuridae is apoikogenic (Francke 1981) therefore it is assumed that *Cercophonius squama* is apoikogenic. Little attention has been given to the embryology of scorpions and species comparisons usually consist of post-partum details: number of young, young orientation and mother-young interaction. This is the first time confirmation of apoikogenesis and the birthing behaviours in *Cercophonius squama* have ever been recorded.

5.2 Methods

Scorpions were housed as described in Section 2.3.

5.2.1 Mating

Two pairs were observed under low intensity white light and low intensity red light during courtship. Notes were taken during the courtship and the duration of activities was recorded. Supplemental viewing was carried out through a dissecting microscope. Video taping of one of the pairs was carried out throughout the courtship process.

5.2.2 Parturition

Females that exhibited increased swelling in the mesosomal region during the housing period were checked multiple times during the day for birthing behaviours. Females were left to give birth and young were counted after parturition was over. Exploration of the female reproductive organs by dissection was undertaken.

5.3 Results

5.3.1 Mating

During my investigation two male to female mating interactions were observed. Several other individuals attempted to mate but did not progress beyond the initial stage. The first display was an unsuccessful attempt that lasted 30 minutes and the second was a successful attempt that lasted 8 hours. Success was considered to be deposition of a spermatophore and uptake of the sperm by the female.

In *Cercophonius squama*, the male initiates the mating process with his approach of the female. Initial contact is an aggressive interaction between the two. The male attempts to grasp the pedipalps of the female with his pedipalps. The female carries a defensive posture and attempts to pull away. As the interactions proceed, the male and female attempt to sting each other. Both animals maintain their position with aggressive movements of their metasoma toward each other. Once the male has a grip on the female's pedipalps, he continues to be aggressive by attempting to sting or threatening to sting the female (Figure 5.1). This stinging does not appear to be a true sting as used in prey capture or male to male encounters but rather a display of dominance. The male uses his metasoma and sting more as a baton to threaten the female. The female uses her sting and metasoma in a similar fashion. The main feature of this stage of the courtship is that the female is continually attempting to break free of the pedipalp grip the male has on her. During this stage one or both of the individuals may be turned over on their side because of the extreme physical interaction. This was the initial stage of the courtship and lasted for less than three minutes.

Figure 5.1 Pedipalp to pedipalp grip of *Cercophonius squama* during courtship; male at the top of picture, female at the bottom.

The next stage is the longest and most complex of all the characteristic sequence of events. The male has demonstrated his dominance over the female and she has accepted him as a suitable mate by ceasing to resist. The female becomes submissive to the male while maintaining a rigid posture. The male begins his movement by pushing and pulling of the grip he has on the female's pedipalps. This push-pull effort by the male is vigorous. Associated with this pedipalp interaction, the male begins to move his "walking legs" back and forth in an attempt to move the female. Eventually he is successful in moving the female around the arena. His pectines move out from underneath him at this stage (Figure 5.2). The pectines are outstretched laterally and moving vertically underneath him. He continues to move the female around the arena with her continuing to be submissive. The male's pectines appear to be sweeping the substrate. Sweeping is the lateral movement of the pectines across the substrate. The male is apparently using his pectines to search for a suitable place to deposit his spermatophore. This search occurs over the entire arena with the male dragging the female across the different substrates and textures throughout the arena. This stage of mating is considered to be the mating dance itself. During this mating dance the female maintains a rigid posture. Her legs are stilted and her metasoma is curled or straight out. Her legs create friction against the substrate and no pectinal movement is observed in the female. The pectines of the male demonstrate an extensive vertical movement that can be termed tapping. Several pauses or breaks in the dance occur with no change in the female but apparent resting by the male. It appears the male uses this time to recuperate from his extensive physical exertions. In the later stages of the dance, the male exhibits a few new movements.

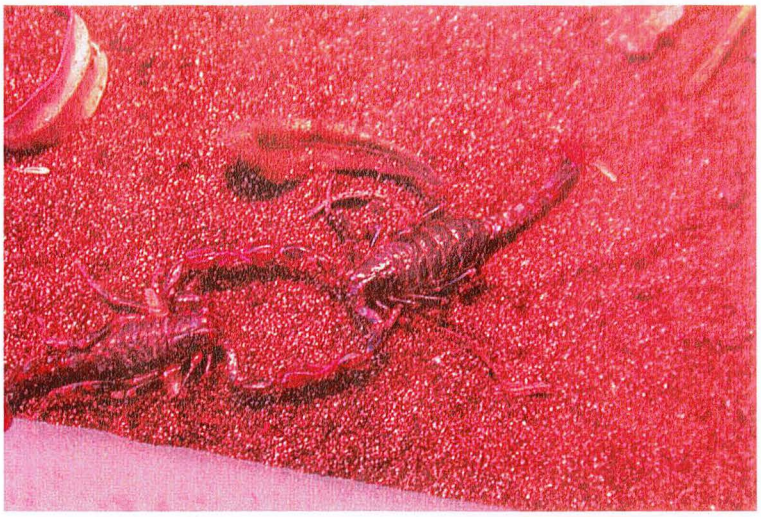

Figure 5.2 Outstreched pectines of the male scorpion (left) *Cercophonius squama* during the mating dance

The sexual sting occurs towards the end of the dance. This sting is not an aggressive attempt by the male but rather a strategic placement of his sting, and occurs during a resting stage of the dance. The male lifts his sting over his head and to the side until it is near the female. At first the female does seem to react or acknowledge the male's sting. Then she lifts her sting in a slow unmotivated action that is not directed. He inserts the sting in the pleural membrane to the side of her carapace on the prosoma (Figure 5.3). The sting is left in place for several seconds. Once the male has inserted his sting into her, she gradually lowers her own sting and appears to settle. The male retracts the sting, and then repeats the sexual sting on the female. Once the sexual sting is over, the female appears to be more submissive than she was before. It is unknown what, if anything, the male transfers during the sexual sting. The stance of the female becomes more relaxed with less resistance than before. The male then begins the dance around the arena with less resistance from the female.

Figure 5.3 Sexual sting of *Cercophonius squama* by the male (right) during mating.

During the second part of the dance the male drags around the more submissive female in a more aggressive manner. This stage of the dance has more resting breaks involved with it. The male seems to be more motivated in finding a suitable place to deposit his spermatophore.

Once the male has found a suitable place to deposit his spermatophore, he begins to massage the chelicera of the female (Figure 5.4). This action is carried out while he still has a grip on the female's pedipalps. The pedipalps are now to the side or outstretched laterally with the very anterior portion of the scorpions' bodies facing each other. The male uses his chelicerae to massage or kiss the chelicerae of the female over and over again. During this time the female is very submissive. She does not cooperate but is absolutely motionless, at the mercy of the male. The reason for lack of movement by the female is unknown. She appears to be almost paralysed during this time.

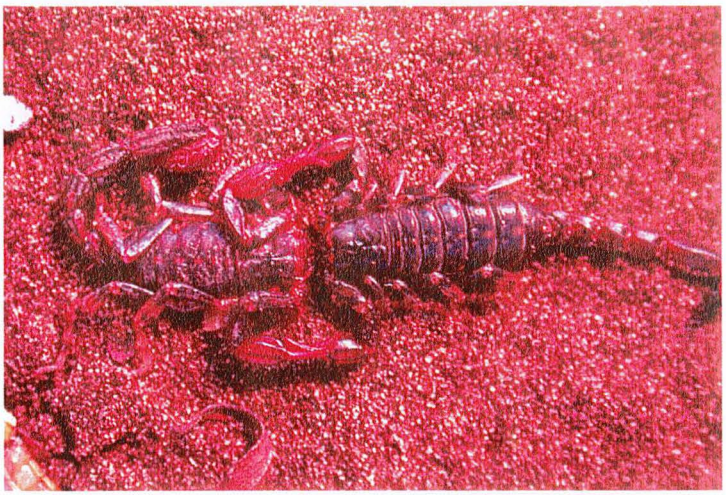

Figure 5.4 Male (left) *Cercophonius squama* massaging the chelicera of the female (right) during the mating process.

The male begins to deposit his spermatophore by rocking his body back and forth over the deposition site. He cements his spermatophore to the substrate and backs off from the site extruding the rest of the spermatophore. Once the spermatophore is deposited the male proceeds to pull the female onto it. This process takes several minutes to properly guide the female onto the spermatophore. The male uses a cheliceral grip at this stage to guide the female. The pedipalps still have contact but the male achieves the most pulling from the cheliceral grip. Several attempts were needed for the female to be manipulated into a position where her gonopore could receive the spermatophore and subsequent uptake of sperm. The female takes the spermatophore up into her gonopore but it does not stay in her at this time. The pressure of the female's body weight achieves the emptying of the spermatophore. Her body weight compresses the spermatophore and forces the sperm from the spermatophore up inside her. The spermatophore is then left in place as both animals back away (Figure 5.5).

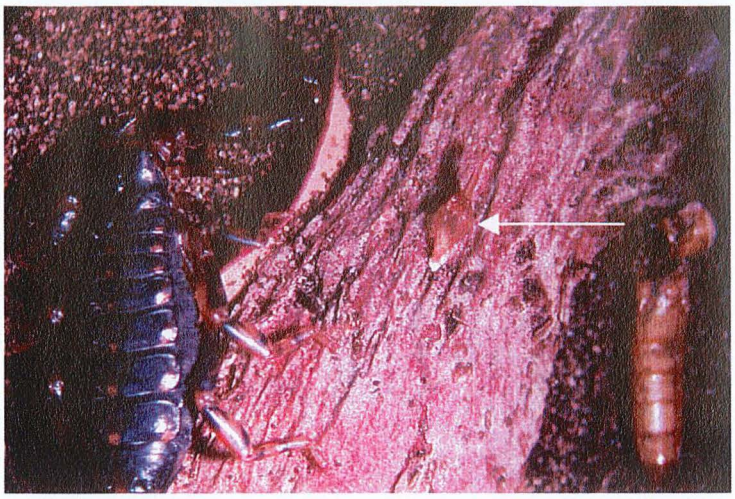

Figure 5.5 Spermatophore of the male scorpion *Cercophonius squama* cemented to a piece of bark during mating.

5.3.2 Birthing

Approximately 10 females were dissected that had developed oocytes associated with the female ovariuterus. The oocytes were located within follicles on the ovariuterus, confirming apoikogenic development.

Parturition was observed in five females, three of which were observed from start to finish. In the three females observed through the entirety, birth began at 12:30 on 8/01, 21:45 on 17/01 and 15:56 on 4/02, and lasted between 4 to 8 hours. Females gave birth to 21-35 young that were orientated both head and tail first at birth. All five females gave birth within a four-week period in January and February. A sixth female was collected in late April from the Central Highlands region of Tasmania with newborn young on her back. A week prior to birth, the embryos within the female can be seen through the intersegmental membrane of the mesosoma.

In the days leading up to birth, females make a burrow or scrape either under a rock or piece of bark. Females that gave birth demonstrated a change in behaviour once birth occurred. The females were less likely to move when disturbed and more likely to assume a defensive posture. Total movement of the female while carrying young was very limited. Females were observed in the same place and usually the same position everyday while carrying young on their back.

One of the females captured in September was noticed to be pregnant in late December. Her abdomen was distended and small white embryos could be seen through the pleural membrane. In January 2002, parturition seemed near, as the female's mesasoma was extremely swollen. Details of the embryos' orientation could not be seen through the pleural membrane due to the apoikogenic development.

The female was observed to assume a posture similar to that of other species during parturition. The body was strongly arched dorsally: the prosoma lifted off the substrate at an angle of about 45°. The pedipalps were moderately outstretched in front with the fingers slightly open, the last two or three mesosomal segments rested on the substrate, and the metasoma curled over the female. The first two pairs of appendages (walking legs) and in one of the females, the third pair of appendages (walking legs) were flexed under the prosoma, forming the birth basket.

Figure 5.6 Female scorpion *Cercophonius squama* giving birth to live young.

During the next four hours, the birth of 23 young were observed. The emergence of the young varied little other than time and duration of emergence. The female varied her behaviour little during the process. The sequence of events for all the females observed giving birth is summarized as follows.

The female begins the birth process by stilting on her legs. She then begins to arch her prosoma back posteriorly. This arching of her body allows the gonopore to open and facilitates the birth process. Young begin to emerge from the female's gonopore in a sac-like membrane. Young are caught in a birth basket made by the female's front appendages but are eventually deposited on the substrate (Figure 5.6). The young are motionless while their siblings continue to emerge one after another. This process is highly variable between females. The emergence of young can be as quick as a few seconds to as long as 10 minutes. The female does not appear to be resting but the rate at which young emerge is variable and can occur in bursts.

The young begin moving 3-30 minutes after emergence. The sac-like membrane that covers the young at birth does not persist. It seems like a sticky fluid that gradually dries out and disappears. The young stretch out their appendages and, turn back towards the mother and begin climbing. The birth basket, formed by the mother's legs, facilitates the young in their climb to her back. The young stay with the mother, on her back for 2-3 weeks (Figure 5.7). They begin to darken or sclerotize their exoskeleton gradually at this stage.

Figure 5.7 Female *Cercophonius squama* with young on her back, one week after birth.

5.4 Discussion

5.4.1 Mating

This is the first time the mating behaviour of *Cercophonius squama* has been recorded. It shows variation from other species, but demonstrates the stereotyped sequence of events, which is scorpion courtship. Table 5.1 compares the behaviours demonstrated by *Cercophonius squama* along with four other bothriurids for which records have been taken.

Interpretation of each behaviour of the courtship has not been carried out. For this reason it cannot be determined what the differences between *Cercophonius squama* and the other bothriurids mean. More replications would be needed to carry out a study of this kind. Records of many mating sequences in the field would be ideal for this type of investigation, but unfortunately it is rare to observe matings in the field. No courtship behaviours were observed in the field during this study. This probably explains the lack of information in the literature concerning the meaning of each sequence of events. Their behaviours are grouped into three Stages for interspecific comparison; initiation, mating dance and spermatophore deposition (Benton 2001). Within these stages, many behaviours are observed. The length of this mating sequence was possibly extended by the laboratory conditions that may not be ideal for spermatophore deposition.

Table 5.1 Courtship and mating behaviours of *Cercophonius squama* from Tasmania in relation to members of the Bothriuridae family from South America.

Taxon: Bothriuridae	Movement	Initiation	_juddering	Clubbing	Pedipalp grip	Cheliceral grip	Sexual sting	Cheliceral massage	_Pecten movement	_Sand scraping	_Headstand	Post mating escape	_Female swaying	Spermatophore Consumed	Mate cannibalism
Bothriurus asper		–	–		+			+	+		+	–			
Bothriurus bonariensis		–	–		+	–									+
Bothriurus flavidus		–			+						+	–		–	
Urophonius brachycentrus		–	–		+	+	+	+	+		+	–		–	+
Cercophonius squama	+	–	–	+	+	+*	+	+	+	–	–	–	–	–	–

Source: Polis & Sissom (1990)
Note: +, behaviour observed; -, behaviour reported to be absent; _, behaviour reported by male; _, behaviour by female; *, behaviour observed during spermatophore deposition (not during the mating dance)

5.4.2 Birth

The birthing process has never been recorded in *Cercophonius squama* until now and it will help elucidate its life history strategies. In turn, the life history strategies can then give clues about the environmental and geological past dictating the evolution of the organism.

Scorpions have few apomorphic characters and their phylogeny has been the centre of many taxonomic debates (Wheeler & Hayashi 1998, Prendini 2000). Birthing behaviours are interrelated in scorpion taxa (Williams 1969) and can help explicate their phylogenetic relationships. Table 5.2 compares the observations of birthing behaviours of *Cercophonius squama* with the only other bothriurid records.

Table 5.2 Parameters of parturition in *Cercophonius squama* from Tasmania and members of the family Bothriuridae from South America.

Taxon	Gestation Period (months)	Duration of Parturition (hrs.)	Date of Birth (month)	Orientation (head or tail)	Litter Size
Bothriurus bonariensis (C.L. Koch)	12	Several	12		41 (35-48)
Urophonius brachycentrus (Pocock)	6.5		11-1	?	33 (21-46)
Urophonius granulatus (Pocock)	9-10		12-1		
Urophonius iheringi (Pocock)	10-11		8-2		47 (31-60)
Cercophonius squama (Gervais)	10-13	4-8	1-4	H-T	28 (21-35)

Sources: Francke 1982 & Polis & Sissom (1990)

Variation in the time of year parturition occurs in *Cercophonius squama* can probably be explained by the environment. All females that were observed giving birth during the four week period were collected from the Hobart area and would have experienced similar climatic conditions. The female collected with young on her back

in late April was from the Central Highlands, which has a colder climate than the Hobart area. This could suggest that scorpions demonstrate a geographic variation in reproduction, similar to that seen in Tasmanian lizards (Wapstra and Swain 2001).

The data collected from these observations will be useful to future reproductive investigations. Manipulative experiments on the affects of environment on reproduction can now be realised. Further investigation would be beneficial to our knowledge of *C. squama* and to the general knowledge of the order.

Chapter 6

Distribution

6.1 Introduction

The distribution of species has long been a concern for biologists. It is important to taxonomic work (Mayr 1963, 1970), population biology (MacArthur & Wilson 1967), evolutionary theory (Wallace 1880) and conservation issues. *Cercophonius squama* has received little scientific attention and its known distribution in Tasmania can be attributed to other invertebrate investigations which have inadvertently gathered data on scorpions.

The aim of this part of the study was to work with Tasmanian Parks and Wildlife Service (GIS Section) to develop a predictive model of the distribution of *Cercophonius squama* in Tasmania.

6.2 Methods

Known distributional records (Figure 6.1) were used to derive a predictive model of distribution. The model used was the Interim Biogeographical Regionalisation for Australia (IBRA5). It was developed in 1998 by David Peters and Richard Thackway for Tasmanian Parks and Wildlife Service GIS Section and the Natural Heritage Trust (Peters & Thackway 1998). This regionalisation is used by the National Reserve System Program (NRS) to provide a national overview for Australia's biodiversity protection. This is an ecosystem-based, regional biogeographical model designed to reflect the spatial organisational of biota (Thackway & Cresswell 1995).

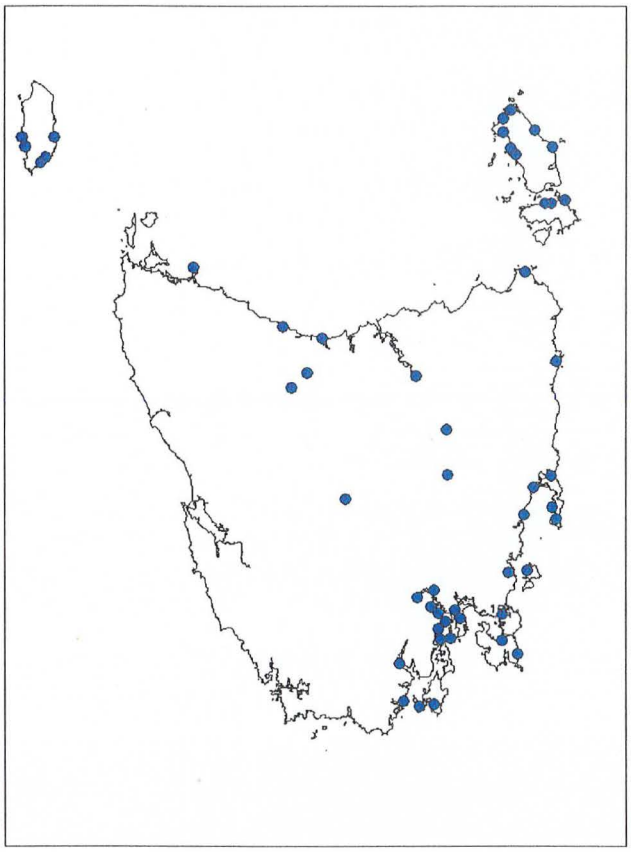

Figure 6.1 Known distribution of *Cercophonius squama* in Tasmania according to museum and pitfall trap records from across the state.

It is derived from a specialized purpose database, GTSpot, that uses few mandatory fields for relating data. The fields that were supplied to Parks are listed below.

GTSpot's mandatory fields are:

Geo reference (geographical coordinates)

Temporal reference (date of observation)

Species (taxonomic) reference

Tag (source reference linking the record to its source)

From these data, the modelling tool CORTEX was used to develop a species range model. Cortex has evolved from BIOCLIM, climate-based modelling, and GARP, a rule based genetic algorithm (Peters & Tackway 1998). The environmental variables used to model a species range include climate, topography and substrate (Table 6.1).

Table. 6.1 Environmental variables used in the IBRA5 model to create a theoretical distribution of *Cercophonius squama* in Tasmania.

Climate	**Topography**	**Substrate**
Mean annual temperature	Elevation (two resolutions)	Geology
Seasonality of temperature	Slope	Potential nutrient
Mean annual rainfall	Aspect (one of many expert models)	Soil Wetness
Seasonality of rainfall	Relief	

6.3 Results

A naïve model for *Cercophonius squama* was developed for Tasmania from these known distribution records throughout the state. The shaded areas of the naïve model represent the predicted distribution of *C. squama* (Fig. 6.2).

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6.3 Results

A naïve model for *Cercophonius squama* was developed for Tasmania from these known distribution records throughout the state. The shaded areas of the naïve model represent the predicted distribution of *C. squama* (Fig. 6.2).

Figure 6.2 A naïve prediction of the distribution of *Cercophonius squama* in Tasmania, produced from the IBRA5 model.

6.4 Discussion

The naïve distribution model reflects the potential distribution of the species with respect to the environmental factors listed in Table 5.1. The model relies on an accurate set of locality records and provides a framework for future refinement. The model does not take into account the specific biology of the species under consideration, but does consider geographical trends of other organisms and the geologic past. The faunal breaks of invertebrates that contributed to the design of the IBRA5 model are demonstrable, but faunal provinces may not be (Mesibov 1994). Subjective modification by experts helps to compensate for this; e.g. crayfish, the genera *Ombrastacoides* and *Spinastacoides* are predicted to be found in the Ben Lomond region of northeast Tasmania but the midlands are an environmental barrier and the genera are restricted to the western part of the state (B. Hansen pers. comm.).

Refinements to the model are needed to accommodate localities that were excluded, as outliers, during its formation. These outliers are probably caused by under sampling of a particular region. For example, a female with young was found recently, near Waddamana in the Central Highlands, indicating that scorpions inhabit this area, although it does not appear in the prediction. Under representation in other areas is harder to explain; for example the Hobart area has many scorpions but is weakly predicted as a suitable site. The strong prediction for the Bass Strait islands is probably due to the preponderance of records from the area.

Exclusions from the prediction are far harder than making additions. Until a location has been sampled, we cannot say with certainty that scorpions do not occur there. However, the purpose of the model is to provide a basis for reasonable prediction. This has then to be evaluated by careful sampling. It is difficult to say what constitutes adequate sampling, but certainly more than one sampling programme needs to be done before excluding a locality. Information from other studies, such as pitfall traps run by DPIWE and personal communication with other scientists can be very useful in developing the expert model. Figure 4.2 shows two areas that are unlikely localities for scorpions to be found. This judgement is based on the absence of records from these areas, their remoteness and the reasonably poor dispersal ability of scorpions. The junction of the Picton and Huon rivers represents an area where the model predicted scorpions could be found but should be excluded. This can be done because over 500 pitfall traps have been run in this area with no scorpion captures (S. Baker, University of Tasmania, pers. comm.)

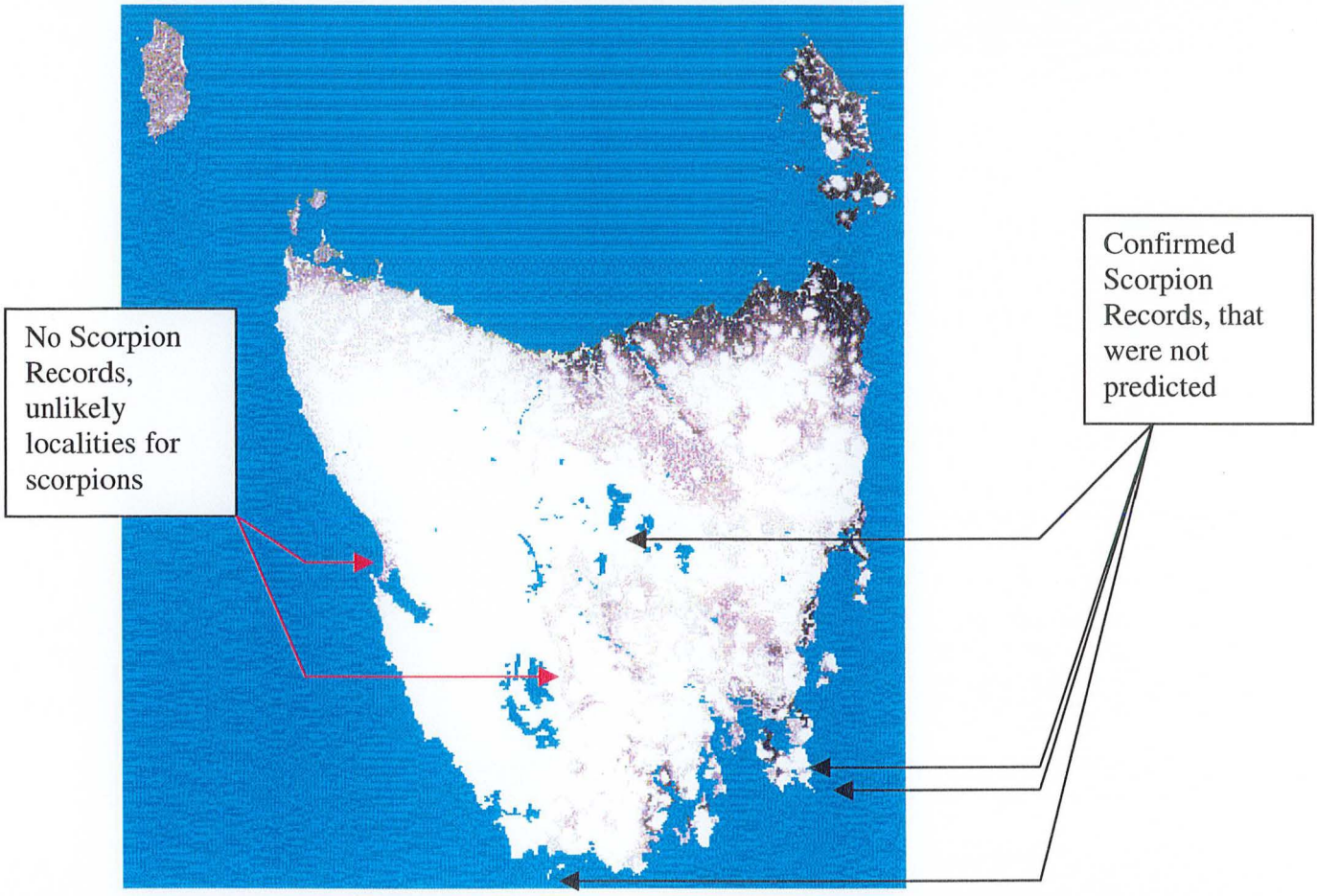

Figure 6.3 A naïve model of the predicted distribution of *Cercophonius squama* in Tasmania with subjective comments about modifications to the prediction.

Chapter 7

General Discussion

This project has provided insight into the biology of *Cercophonius squama.* The southerly, colder, more variable climate in Tasmania has implications for scorpions and their prey. The harsh winter conditions, short duration of summer and the cooler temperatures can have a number of consequences for poikilothermic animals like scorpions. In most temperate species of scorpions, activity occurs during the warmer months, with peaks in May and September for Northern Hemisphere scorpions. There are insufficient data on Southern Hemisphere species to detect any trends in peak activity, while the bothriurid *Urophonius brachycentrus* demonstrates the most activity during the winter (Polis & Sissom 1990). This demonstrates the need for further ecological studies in the Southern Hemisphere. The investigation has acquired baseline knowledge that will make future investigations possible.

The rich natural diversity of scorpions from temperate to tropical habitats and their lack of ability to disperse on a geographical scale make them good subjects for analysis of geographical distribution (Brownell 2001). Most scorpion studies have been conducted in desert communities, where the number of genera is highest. This has provided insight into the general ecology of the order but does not necessarily provide information about scorpion biology in very different habitats.

Cercophonius squama provides an opportunity to investigate the ability of scorpions to adapt to cool-temperate environments. Much of my data will be helpful in this regard. For example, with 100% reliability, it is now possible to identify the sex of a population using the cusp, which is vital for future ecological investigations. The

lifecycle can partially be inferred from the reproductive behaviours and seasonal activity patterns of this scorpion. It is unlikely that females give birth every year because of the timing of birth and mating. Females would hardly have time to recover from the birth to mate the same year. Most likely, only a small proportion of the females are reproducing each year.

Scorpions demonstrate k-selected life history strategies more universally than other arthropod groups. *Cercophonius squama* does not appear to be an exception to this generalisation of scorpions. There are several features that qualify scorpions as a k-selected or equilibrium species. An equilibrium species develops slowly to a relatively large size and produces (for a series of years) relatively few offspring, each of which represents a relatively large parental investment; survivorship is Type 1 or 2 (Polis 1980); mortality is predominately density-dependent and the magnitude of population fluctuation is relatively small; they inhabit predictable environments in which species interactions are a paramount force; and occupy a narrow, specialized niche (MacArthur and Wilson 1967).

Cercophonius squama has an extremely long gestation period, unusual for invertebrates and approaching gestation periods close to that of the largest land mammals. There is a large variation in scorpions and gestation times vary from 1.5 months in *Orthochirus innesi* to 18 months by two species of *Opisthacanthus* (Polis & Sissom 1990). *Cercophonius squama* falls in the middle of the spectrum with a gestation period of at least 10 months. The subsequent maturation process may also be lengthy in *Cercophonius squama*. Smith (1966) noted that *Urodacus abruptus* does not reproduce until its 3rd year and has a gestation period of 16 months, after which

the young stay with the female for a further month. The time to complete both periods contributes to a long generation time and a very low net reproductive rate. Smith (1966) reported the generation time for *U. abruptus* as 5.13 years with a reproductive rate of 1.50 per generation, which means a population could only increase by 50% in a 5-year period. With reproductive rates this low, there is a real risk of extinction when there are high levels of sustained disturbance.

We now have a record of the mating behaviours of *C. squama* in Tasmania, which is only the third such description for an Australian scorpion. It represents the only record of bothriurid mating behaviour outside of South America.

Identical behaviours are frequently observed in scorpion species that are only distantly related suggesting that reproductive behaviour is conservative in this group and appeared at a point in scorpion evolution before the various modern families diverged (Polis & Sissom 1990). Until the study by Benton (2001) of *Leiurus quinquestriatus*, there had not been a detailed study to ascertain the functions of the component behaviours in scorpion courtship. He concluded that the reproductive behaviours of scorpions are more complex than first thought and this field of study needs to be further investigated.

Scorpion biology is complex and the investigations have just begun to demonstrate the importance of the group. It is obvious that more investigations need to be carried out to gain insight into the complexities of the biology of *Cercophonius squama.* When this investigation began we had a blank sheet that needed to be filled in. The general understanding of the biology of *C. squama* was assumed from the family.

Many of the questions such as where they occur, what their fecundity is like, how long is gestation, and when they are active, have been resolved.

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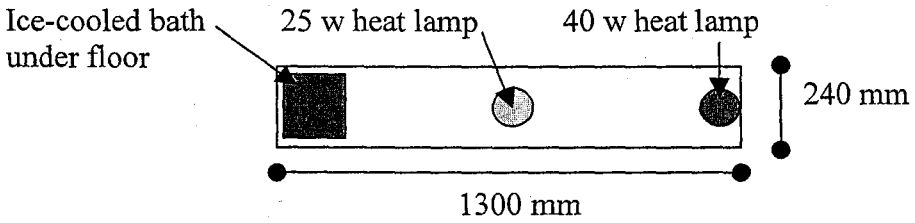
Appendix 1 Temperature Trials

Method

An aluminium box (1300 x 240 x 190 mm) was used as the experimental chamber. One end of the chamber was equipped with a cooling system through which water was pumped after being cooled in an ice-bath. Two heat lamps were used (25 & 40 watt bulbs) positioned below the floor of the chamber approximately 400 mm apart providing increasing levels of heat away from the cooled area. This created a temperature gradient of approximately 8.0 °C to 27 °C. A skeletal soil substrate from the field site was provided; however no food, shelter or water was provided. The experiment was performed in the laboratory at ambient temperature.



Trials began at approximately 8:00 pm and continued to 10am the next morning. Scorpions were placed in a random direction and location within the chamber. They were given one hour to acclimate to the chamber before records of the location were taken. Locations of the scorpion were recorded every thirty minutes for the first three hours, then every hour for the next two hours and then again the following morning. Temperatures for the locations were determined with the use of four thermometers placed throughout the chamber. A thermometer was moved near the location of the scorpion to determine the temperature at a given time. Scorpions are extremely

aggressive and even cannibalistic, so only one scorpion was tested per trial. The temperature the animals selected for the majority of the time was considered the preferred temperature.

Results Temperature

All scorpions initially responded by actively moving throughout the chamber. Scorpions from the greater Hobart area demonstrated a temperature preference for temperatures lower than 18° C. Scorpions were observed moving across all areas but the majority of activity and resting records were from regions with temperatures less than 18° C. The results from the temperature trials were however, inconclusive and abandoned.

4.3 Discussion

Temperature

The temperature preference set up was not appropriate for the specimen due to the construction of the housing in regards to the size of the animal. It was originally used to test temperature preferences in lizards. The set up was laterally gradient (fig 4.3). This lateral gradient would not affect the trials with lizards that are many times larger than scorpions. The larger lizards would have some portion of their body over the centre gradient and therefore be affected by that temperature regime. By contrast, scorpions could have their entire body away from the centre gradient and not be affected by that temperature regime. This created a gradient laterally across the chamber that would not be perceived by lizards but would likely have a large affect on scorpions. Thermometers were placed near the scorpion to record the specific temperature but a lag time occurred and if the scorpion moved the temperature

reading was not accurate. With lizards, a thermometer was inserted into the cloaca to record preferred body temperatures (Kabat 1999), thus, avoiding any complications presented by a lateral gradient. This is not possible for scorpions and equipment was not available to record temperatures throughout the arena, so determining temperature preferences was not viable. A smaller design would help to eliminate this lateral gradient for scorpions.

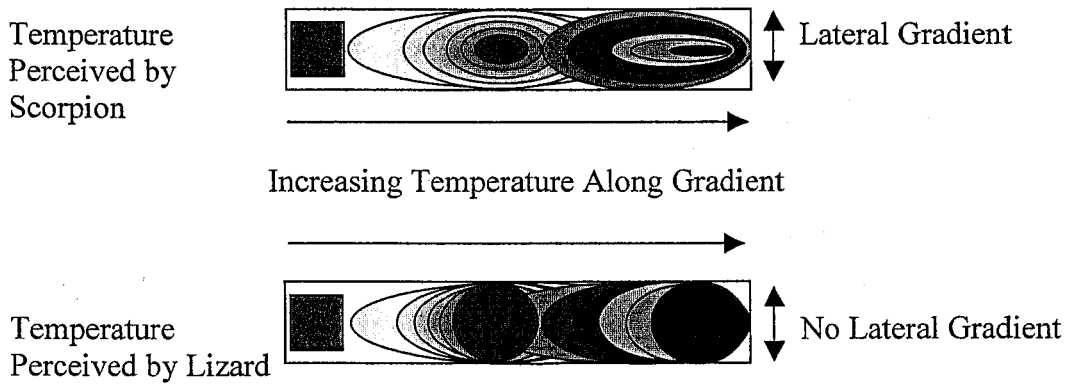


Figure 4.3 Possible temperature effects on Scorpions as compared to Lizards

Appendix 2 MANOVA

Multivariate Tests

Effect		Value	F	Hypothesis df	Error df	Sig.
Intercept	Pillai's Trace	.999	12936.243	7.000	133.000	.000
Intercept	Pillai's Trace	.999	12936.243	7.000	133.000	.000
	Wilks' Lambda	.001	12936.243	7.000	133.000	.000
	Wilks' Lambda	.001	12936.243	7.000	133.000	.000
	Hotelling's Trace	680.855	12936.243	7.000	133.000	.000
	Hotelling's Trace	680.855	12936.243	7.000	133.000	.000
	Roy's Largest Root	680.855	12936.243	7.000	133.000	.000
	Roy's Largest Root	680.855	12936.243	7.000	133.000	.000
SEX	Pillai's Trace	.432	14.425	7.000	133.000	.000
SEX	Pillai's Trace	.432	14.425	7.000	133.000	.000
	Wilks' Lambda	.568	14.425	7.000	133.000	.000
	Wilks' Lambda	.568	14.425	7.000	133.000	.000
	Hotelling's Trace	.759	14.425	7.000	133.000	.000
	Hotelling's Trace	.759	14.425	7.000	133.000	.000
	Roy's Largest Root	.759	14.425	7.000	133.000	.000
	Roy's Largest Root	.759	14.425	7.000	133.000	.000

a Exact statistic
b Design: Intercept+SEX

Tests of Between-Subjects Effects

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	CW	3.256E-04	1	3.256E-04	.082	.775
Corrected Model	CW	3.256E-04	1	3.256E-04	.082	.775
	LH	6.187E-02	1	6.187E-02	17.046	.000
	LH	6.187E-02	1	6.187E-02	17.046	.000
	HFF	.243	1	.243	41.016	.000
	HFF	.243	1	.243	41.016	.000
	MF	8.081E-03	1	8.081E-03	1.968	.163
	MF	8.081E-03	1	8.081E-03	1.968	.163
	WH	3.715E-02	1	3.715E-02	41.883	.000
	WH	3.715E-02	1	3.715E-02	41.883	.000

	FOURTH	.146	1	.146	32.710	.000
	FIFTH	.355	1	.355	41.853	.000
	FIFTH	.355	1	.355	41.853	.000
Intercept	CW	208.909	1	208.909	52742.442	.000
Intercept	CW	208.909	1	208.909	52742.442	.000
	LH	65.420	1	65.420	18023.879	.000
	LH	65.420	1	65.420	18023.879	.000
	HFF	307.193	1	307.193	51861.750	.000
	HFF	307.193	1	307.193	51861.750	.000
	MF	109.311	1	109.311	26613.400	.000
	MF	109.311	1	109.311	26613.400	.000
	WH	30.381	1	30.381	34252.230	.000
	WH	30.381	1	30.381	34252.230	.000
	FOURTH	62.936	1	62.936	14115.351	.000
	FOURTH	62.936	1	62.936	14115.351	.000
	FIFTH	167.772	1	167.772	19783.408	.000
	FIFTH	167.772	1	167.772	19783.408	.000
SEX	CW	3.256E-04	1	3.256E-04	.082	.775
SEX	CW	3.256E-04	1	3.256E-04	.082	.775
	LH	6.187E-02	1	6.187E-02	17.046	.000
	LH	6.187E-02	1	6.187E-02	17.046	.000
	HFF	.243	1	.243	41.016	.000
	HFF	.243	1	.243	41.016	.000
	MF	8.081E-03	1	8.081E-03	1.968	.163
	MF	8.081E-03	1	8.081E-03	1.968	.163
	WH	3.715E-02	1	3.715E-02	41.883	.000
	WH	3.715E-02	1	3.715E-02	41.883	.000
	FOURTH	.146	1	.146	32.710	.000
	FOURTH	.146	1	.146	32.710	.000
	FIFTH	.355	1	.355	41.853	.000
	FIFTH	.355	1	.355	41.853	.000
Error	CW	.551	139	3.961E-03		
Error	CW	.551	139	3.961E-03		
	LH	.505	139	3.630E-03		
	LH	.505	139	3.630E-03		
	HFF	.823	139	5.923E-03		
	HFF	.823	139	5.923E-03		
	MF	.571	139	4.107E-03		
	MF	.571	139	4.107E-03		
	WH	.123	139	8.870E-04		
	WH	.123	139	8.870E-04		
	FOURTH	.620	139	4.459E-03		
	FOURTH	.620	139	4.459E-03		
	FIFTH	1.179	139	8.480E-03		
	FIFTH	1.179	139	8.480E-03		
Total	CW	250.521	141			
Total	CW	250.521	141			
	LH	80.723	141			
	LH	80.723	141			
	HFF	376.665	141			
	HFF	376.665	141			
	MF	132.154	141			
	MF	132.154	141			
	WH	37.510	141			
	WH	37.510	141			
	FOURTH	78.952	141			
	FOURTH	78.952	141			
	FIFTH	209.606	141			
	FIFTH	209.606	141			
Corrected	CW	.551	140			

Total			
	LH	.566	140
	LH	.566	140
	HFF	1.066	140
	HFF	1.066	140
	MF	.579	140
	MF	.579	140
	WH	.160	140
	WH	.160	140
	FOURTH	.766	140
	FOURTH	.766	140
	FIFTH	1.534	140
	FIFTH	1.534	140

a R Squared = .001 (Adjusted R Squared = -.007)
b R Squared = .109 (Adjusted R Squared = .103)
c R Squared = .228 (Adjusted R Squared = .222)
d R Squared = .014 (Adjusted R Squared = .007)
e R Squared = .232 (Adjusted R Squared = .226)
f R Squared = .190 (Adjusted R Squared = .185)
g R Squared = .231 (Adjusted R Squared = .226)

Appendix 2 MANOVA

Multivariate Tests

Effect		Value	F	Hypothesis df	Error df	Sig.
Intercept	Pillai's Trace	.999	12936.243	7.000	133.000	.000
Intercept	Pillai's Trace	.999	12936.243	7.000	133.000	.000
	Wilks' Lambda	.001	12936.243	7.000	133.000	.000
	Wilks' Lambda	.001	12936.243	7.000	133.000	.000
	Hotelling's Trace	680.855	12936.243	7.000	133.000	.000
	Hotelling's Trace	680.855	12936.243	7.000	133.000	.000
	Roy's Largest Root	680.855	12936.243	7.000	133.000	.000
	Roy's Largest Root	680.855	12936.243	7.000	133.000	.000
SEX	Pillai's Trace	.432	14.425	7.000	133.000	.000
SEX	Pillai's Trace	.432	14.425	7.000	133.000	.000
	Wilks' Lambda	.568	14.425	7.000	133.000	.000
	Wilks' Lambda	.568	14.425	7.000	133.000	.000
	Hotelling's Trace	.759	14.425	7.000	133.000	.000
	Hotelling's Trace	.759	14.425	7.000	133.000	.000
	Roy's Largest Root	.759	14.425	7.000	133.000	.000
	Roy's Largest Root	.759	14.425	7.000	133.000	.000

a Exact statistic
b Design: Intercept+SEX

Tests of Between-Subjects Effects

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	CW	3.256E-04	1	3.256E-04	.082	.775
Corrected Model	CW	3.256E-04	1	3.256E-04	.082	.775
	LH	6.187E-02	1	6.187E-02	17.046	.000
	LH	6.187E-02	1	6.187E-02	17.046	.000
	HFF	.243	1	.243	41.016	.000
	HFF	.243	1	.243	41.016	.000
	MF	8.081E-03	1	8.081E-03	1.968	.163
	MF	8.081E-03	1	8.081E-03	1.968	.163
	WH	3.715E-02	1	3.715E-02	41.883	.000
	WH	3.715E-02	1	3.715E-02	41.883	.000

	FOURTH	.146	1	.146	32.710	.000
	FIFTH	.355	1	.355	41.853	.000
	FIFTH	.355	1	.355	41.853	.000
Intercept	CW	208.909	1	208.909	52742.442	.000
Intercept	CW	208.909	1	208.909	52742.442	.000
	LH	65.420	1	65.420	18023.879	.000
	LH	65.420	1	65.420	18023.879	.000
	HFF	307.193	1	307.193	51861.750	.000
	HFF	307.193	1	307.193	51861.750	.000
	MF	109.311	1	109.311	26613.400	.000
	MF	109.311	1	109.311	26613.400	.000
	WH	30.381	1	30.381	34252.230	.000
	WH	30.381	1	30.381	34252.230	.000
	FOURTH	62.936	1	62.936	14115.351	.000
	FOURTH	62.936	1	62.936	14115.351	.000
	FIFTH	167.772	1	167.772	19783.408	.000
	FIFTH	167.772	1	167.772	19783.408	.000
SEX	CW	3.256E-04	1	3.256E-04	.082	.775
SEX	CW	3.256E-04	1	3.256E-04	.082	.775
	LH	6.187E-02	1	6.187E-02	17.046	.000
	LH	6.187E-02	1	6.187E-02	17.046	.000
	HFF	.243	1	.243	41.016	.000
	HFF	.243	1	.243	41.016	.000
	MF	8.081E-03	1	8.081E-03	1.968	.163
	MF	8.081E-03	1	8.081E-03	1.968	.163
	WH	3.715E-02	1	3.715E-02	41.883	.000
	WH	3.715E-02	1	3.715E-02	41.883	.000
	FOURTH	.146	1	.146	32.710	.000
	FOURTH	.146	1	.146	32.710	.000
	FIFTH	.355	1	.355	41.853	.000
	FIFTH	.355	1	.355	41.853	.000
Error	CW	.551	139	3.961E-03		
Error	CW	.551	139	3.961E-03		
	LH	.505	139	3.630E-03		
	LH	.505	139	3.630E-03		
	HFF	.823	139	5.923E-03		
	HFF	.823	139	5.923E-03		
	MF	.571	139	4.107E-03		
	MF	.571	139	4.107E-03		
	WH	.123	139	8.870E-04		
	WH	.123	139	8.870E-04		
	FOURTH	.620	139	4.459E-03		
	FOURTH	.620	139	4.459E-03		
	FIFTH	1.179	139	8.480E-03		
	FIFTH	1.179	139	8.480E-03		
Total	CW	250.521	141			
Total	CW	250.521	141			
	LH	80.723	141			
	LH	80.723	141			
	HFF	376.665	141			
	HFF	376.665	141			
	MF	132.154	141			
	MF	132.154	141			
	WH	37.510	141			
	WH	37.510	141			
	FOURTH	78.952	141			
	FOURTH	78.952	141			
	FIFTH	209.606	141			
	FIFTH	209.606	141			
Corrected	CW	.551	140			

Total			
	LH	.566	140
	LH	.566	140
	HFF	1.066	140
	HFF	1.066	140
	MF	.579	140
	MF	.579	140
	WH	.160	140
	WH	.160	140
	FOURTH	.766	140
	FOURTH	.766	140
	FIFTH	1.534	140
	FIFTH	1.534	140

a R Squared = .001 (Adjusted R Squared = -.007)
b R Squared = .109 (Adjusted R Squared = .103)
c R Squared = .228 (Adjusted R Squared = .222)
d R Squared = .014 (Adjusted R Squared = .007)
e R Squared = .232 (Adjusted R Squared = .226)
f R Squared = .190 (Adjusted R Squared = .185)
g R Squared = .231 (Adjusted R Squared = .226)

Appendix 3 Discriminant Function Analysis without carapace width in the analysis.

Stepwise Statistics

Wilks' Lambda

Step	Number of Variables	Lambda	df1	df2	df3	Exact F Statistic	df1	df2	
Step						Statistic	df1	df2	
1	1	.768	1	1	139	41.883	1	139.000	1.531
1	1	.768	1	1	139	41.883	1	139.000	1.531
2	2	.662	2	1	139	35.194	2	138.000	4.414
2	2	.662	2	1	139	35.194	2	138.000	4.414
3	3	.635	3	1	139	26.257	3	137.000	1.622
3	3	.635	3	1	139	26.257	3	137.000	1.622

Summary of Canonical Discriminant Functions

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	.575	100.0	100.0	.604
1	.575	100.0	100.0	.604

a First 1 canonical discriminant functions were used in the analysis.

Wilks' Lambda

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1	.635	62.457	3	.000
1	.635	62.457	3	.000

Standardized Canonical Discriminant Function Coefficients

	Function
	1
	1
HFF	.377
HFF	.377
WH	.535
WH	.535
FIFTH	.474
FIFTH	.474

Structure Matrix

	Function
	1
	1
WH	.724
WH	.724
FIFTH	.724
FIFTH	.724
HFF	.716
HFF	.716
FOURTH	.408
FOURTH	.408
LH	.367
LH	.367

Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions Variables ordered by absolute size of correlation within function.
a This variable not used in the analysis.

Classification Statistics

Classification Function Coefficients

	SEX	
	1.00	2.00
	1.00	2.00
HFF	211.317	203.248
HFF	211.317	203.248
WH	413.666	384.114
WH	413.666	384.114
FIFTH	51.129	42.662
FIFTH	51.129	42.662
(Constant)	-316.527	-278.410
(Constant)	-316.527	-278.410

Fisher's linear discriminant functions

Casewise Statistics

		Actual Group	Highest Group				Second Highest Group			Discriminant Scores
			Predicted Group	P(D>d | G=g)	P(G=g | D=d)	Squared Mahalanobis Distance to Centroid	Group	P(G=g | D=d)	Squared Mahalanobis Distance to Centroid	Function 1
			Predicted Group	P(D>d | G=g)	P(G=g | D=d)	Squared Mahalanobis Distance to Centroid	Group	P(G=g | D=d)	Squared Mahalanobis Distance to Centroid	Function 1
	Case Number			pdf						
	Case Number			pdf						
Original	1	1	1	.682	1 .664	.168	2	.336	1.528	.080
Original	1	1	1	.682	1 .664	.168	2	.336	1.528	.080
	2	2	2	.775	1 .708	.081	1	.292	1.852	-.871
	2	2	2	.775	1 .708	.081	1	.292	1.852	-.871
	3	1	1	.442	1 .522	.591	2	.478	.770	-.279
	3	1	1	.442	1 .522	.591	2	.478	.770	-.279
	4	2	2	.718	1 .875	.130	1	.125	4.030	-1.517
	4	2	2	.718	1 .875	.130	1	.125	4.030	-1.517
	5	2	2	.743	1 .693	.107	1	.307	1.738	-.828
	5	2	2	.743	1 .693	.107	1	.307	1.738	-.828
	6	2	1	.585	1 .612	.298	2	.388	1.210	-.056
	6	2	1	.585	1 .612	.298	2	.388	1.210	-.056
	7	2	2	.901	1 .759	.016	1	.241	2.315	-1.031
	7	2	2	.901	1 .759	.016	1	.241	2.315	-1.031
	8	2	1	.533	1 .581	.389	2	.419	1.046	-.133
	8	2	1	.533	1 .581	.389	2	.419	1.046	-.133
	9	1	1	.203	1 .969	1.618	2	.031	8.517	1.763
	9	1	1	.203	1 .969	1.618	2	.031	8.517	1.763
	10	1	1	.149	1 .977	2.081	2	.023	9.541	1.933
	10	1	1	.149	1 .977	2.081	2	.023	9.541	1.933
	11	1	1	.853	1 .741	.034	2	.259	2.134	.305

12	1	1	.432	1	.515	.618	2	.485	.739	-.296
13	2	2	.364	1	.945	.823	1	.055	6.520	-2.063
13	2	2	.364	1	.945	.823	1	.055	6.520	-2.063
14	1	1	.322	1	.952	.979	2	.048	6.948	1.480
14	1	1	.322	1	.952	.979	2	.048	6.948	1.480
15	1	1	.476	1	.546	.507	2	.454	.872	-.222
15	1	1	.476	1	.546	.507	2	.454	.872	-.222
16	1	1	.767	1	.863	.088	2	.137	3.775	.787
16	1	1	.767	1	.863	.088	2	.137	3.775	.787
17	1	1	.105	1	.982	2.626	2	.018	10.672	2.111
17	1	1	.105	1	.982	2.626	2	.018	10.672	2.111
18	1	1	.350	1	.948	.873	2	.052	6.659	1.425
18	1	1	.350	1	.948	.873	2	.052	6.659	1.425
19	2	2	.525	1	.577	.404	1	.423	1.022	-.521
19	2	2	.525	1	.577	.404	1	.423	1.022	-.521
20	1	1	.645	1	.645	.212	2	.355	1.407	.030
20	1	1	.645	1	.645	.212	2	.355	1.407	.030
21	1	1	.326	1	.951	.963	2	.049	6.905	1.472
21	1	1	.326	1	.951	.963	2	.049	6.905	1.472
22	1	2	.751	1	.697	.101	1	.303	1.765	-.838
22	1	2	.751	1	.697	.101	1	.303	1.765	-.838
23	1	1	.906	1	.762	.014	2	.238	2.337	.373
23	1	1	.906	1	.762	.014	2	.238	2.337	.373
24	1	1	.140	1	.978	2.183	2	.022	9.758	1.968
24	1	1	.140	1	.978	2.183	2	.022	9.758	1.968
25	1	1	.779	1	.860	.079	2	.140	3.713	.771
25	1	1	.779	1	.860	.079	2	.140	3.713	.771
26	1	1	.919	1	.821	.010	2	.179	3.054	.592
26	1	1	.919	1	.821	.010	2	.179	3.054	.592
27	1	2	.810	1	.723	.058	1	.277	1.976	-.915
27	1	2	.810	1	.723	.058	1	.277	1.976	-.915
28	1	1	.831	1	.846	.046	2	.154	3.458	.704
28	1	1	.831	1	.846	.046	2	.154	3.458	.704
29	1	1	.227	1	.966	1.462	2	.034	8.152	1.699
29	1	1	.227	1	.966	1.462	2	.034	8.152	1.699
30	1	1	.198	1	.970	1.656	2	.030	8.603	1.777
30	1	1	.198	1	.970	1.656	2	.030	8.603	1.777
31	1	2	.680	1	.663	.170	1	.337	1.522	-.743
31	1	2	.680	1	.663	.170	1	.337	1.522	-.743
32	1	1	.684	1	.883	.165	2	.117	4.214	.897
32	1	1	.684	1	.883	,165	2	.117	4.214	.897
33	2	2	.507	1	.920	.441	1	.080	5.336	-1.820
33	2	2	.507	1	.920	.441	1	.080	5.336	-1.820
34	2	2	.942	1	.814	.005	1	.186	2.955	-1.229
34	2	2	.942	1	.814	.005	1	.186	2.955	-1.229
35	2	2	.427	1	.935	.631	1	.065	5.956	-1.950
35	2	2	.427	1	.935	.631	1	.065	5.956	-1.950
36	2	2	.869	1	.747	.027	1	.253	2.195	-.991
36	2	2	.869	1	.747	.027	1	.253	2.195	-.991
37	1	1	.944	1	.813	.005	2	.187	2.945	.560
37	1	1	.944	1	.813	.005	2	.187	2.945	.560
38	2	1	.558	1	.596	.344	2	.404	1.123	-.096
38	2	1	.558	1	.596	.344	2	.404	1.123	-.096
39	1	1	.646	1	.646	.211	2	.354	1.410	.032
39	1	1	.646	1	.646	.211	2	.354	1.410	.032
40	1	1	.367	1	.945	.814	2	.055	6.495	1.393
40	1	1	.367	1	.945	.814	2	.055	6.495	1.393
41	1	1	.774	1	.707	.082	2	.293	1.848	.204
41	1	1	.774	1	.707	.082	2	.293	1.848	.204
42	2	2	.134	1	.979	2.251	1	.021	9.900	-2.656

43	2	2	.500	1	.922	.455	1	.078	5.386	-1.830
44	2	2	.884	1	.831	.021	1	.169	3.212	-1.302
44	2	2	.884	1	.831	.021	1	.169	3.212	-1.302
45	1	1	.900	1	.759	.016	2	.241	2.313	.365
45	1	1	.900	1	.759	.016	2	.241	2.313	.365
46	2	2	.652	1	.891	.204	1	.109	4.401	-1.607
46	2	2	.652	1	.891	.204	1	.109	4.401	-1.607
47	1	2	.456	1	.930	.557	1	.070	5.724	-1.902
47	1	2	.456	1	.930	.557	1	.070	5.724	-1.902
48	2	1	.440	1	.521	.597	2	.479	.763	-.282
48	2	1	.440	1	.521	.597	2	.479	.763	-.282
49	2	1	.487	1	.552	.483	2	.448	.905	-.205
49	2	1	.487	1	.552	.483	2	.448	.905	-.205
50	1	1	.253	1	.962	1.304	2	.038	7.775	1.632
50	1	1	.253	1	.962	1.304	2	.038	7.775	1.632
51	1	1	.714	1	.876	.134	2	.124	4.050	.857
51	1	1	.714	1	.876	.134	2	.124	4.050	.857
52	1	2	.472	1	.543	.516	1	.457	.861	-.437
52	1	2	.472	1	.543	.516	1	.457	.861	-.437
53	1	1	.909	1	.824	.013	2	.176	3.099	.604
53	1	1	.909	1	.824	.013	2	.176	3.099	.604
54	2	2	.740	1	.870	.110	1	.130	3.911	-1.487
54	2	2	.740	1	.870	.110	1	.130	3.911	-1.487
55	1	2	.418	1	.505	.657	1	.495	.699	-.345
55	1	2	.418	1	.505	.657	1	.495	.699	-.345
56	1	1	.627	1	.635	.236	2	.365	1.346	.004
56	1	1	.627	1	.635	.236	2	.365	1.346	.004
57	2	2	.002	1	.998	9.142	1	.002	21.807	-4.179
57	2	2	.002	1	.998	9.142	1	.002	21.807	-4.179
58	1	1	.820	1	.849	.052	2	.151	3.509	.717
58	1	1	.820	1	.849	.052	2	.151	3.509	.717
59	2	1	.573	1	.605	.318	2	.395	1.171	-.074
59	2	1	.573	1	.605	.318	2	.395	1.171	-.074
60	2	1	.573	1	.605	.318	2	.395	1.171	-.074
60	2	1	.573	1	.605	.318	2	.395	1.171	-.074
61	1	1	.847	1	.842	.037	2	.158	3.384	.684
61	1	1	.847	1	.842	.037	2	.158	3.384	.684
62	1	1	.512	1	.568	.431	2	.432	.980	-.166
62	1	1	.512	1	.568	.431	2	.432	.980	-.166
63	1	1	.037	1	.992	4.372	2	.008	13.966	2.581
63	1	1	.037	1	.992	4.372	2	.008	13.966	2.581
64	1	1	.565	1	.909	.331	2	.091	4.934	1.065
64	1	1	.565	1	.909	.331	2	.091	4.934	1.065
65	1	2	.562	1	.910	.337	1	.090	4.957	-1.736
65	1	2	.562	1	.910	.337	1	.090	4.957	-1.736
66	1	1	.519	1	.573	.415	2	.427	1.004	-.154
66	1	1	.519	1	.573	.415	2	.427	1.004	-.154
67	2	2	.361	1	.946	.836	1	.054	6.555	-2.070
67	2	2	.361	1	.946	.836	1	.054	6.555	-2.070
68	1	1	.789	1	.714	.071	2	.286	1.902	.223
68	1	1	.789	1	.714	.071	2	.286	1.902	.223
69	1	1	.633	1	.895	.229	2	.105	4.513	.968
69	1	1	.633	1	.895	.229	2	.105	4.513	.968
70	1	1	.403	1	.939	.699	2	.061	6.160	1.326
70	1	1	.403	1	.939	.699	2	.061	6.160	1.326
71	1	2	.518	1	.572	.418	1	.428	.999	-.509
71	1	2	.518	1	.572	.418	1	.428	.999	-.509
72	1	1	.992	1	.792	.000	2	.208	2.678	.480
72	1	1	.992	1	.792	.000	2	.208	2.678	.480
73	1	2	.568	1	.602	.327	1	.398	1.155	-.584

74	1	1	.330	1	.951	.951	2	.049	6.871	1.465
75	1	1	.656	1	.890	.199	2	.110	4.376	.936
75	1	1	.656	1	.890	.199	2	.110	4.376	.936
76	2	2	.862	1	.838	.030	1	.162	3.311	-1.329
76	2	2	.862	1	.838	.030	1	.162	3.311	-1.329
77	2	2	.068	1	.987	3.320	1	.013	12.029	-2.978
77	2	2	.068	1	.987	3.320	1	.013	12.029	-2.978
78	1	1	.994	1	.793	.000	2	.207	2.687	.483
78	1	1	.994	1	.793	.000	2	.207	2.687	.483
79	1	1	.716	1	.681	.132	2	.319	1.645	.127
79	1	1	.716	1	.681	.132	2	.319	1.645	.127
80	1	2	.505	1	.921	.445	1	.079	5.351	-1.823
80	1	2	.505	1	.921	.445	1	.079	5.351	-1.823
81	1	2	.758	1	.700	.095	1	.300	1.791	-.848
81	1	2	.758	1	.700	.095	1	.300	1.791	-.848
82	1	1	.798	1	.855	.065	2	.145	3.616	.746
82	1	1	.798	1	.855	.065	2	.145	3.616	.746
83	2	2	.702	1	.674	.147	1	.326	1.596	-.773
83	2	2	.702	1	.674	.147	1	.326	1.596	-.773
84	2	2	.850	1	.740	.036	1	.260	2.124	-.967
84	2	2	.850	1	.740	.036	1	.260	2.124	-.967
85	1	1	.467	1	.928	.530	2	.072	5.638	1.219
85	1	1	.467	1	.928	.530	2	.072	5.638	1.219
86	1	1	.714	1	.876	.134	2	.124	4.050	.857
86	1	1	.714	1	.876	.134	2	.124	4.050	.857
87	1	2	.922	1	.820	.010	1	.180	3.043	-1.254
87	1	2	.922	1	.820	.010	1	.180	3.043	-1.254
88	1	1	.192	1	.971	1.701	2	.029	8.706	1.795
88	1	1	.192	1	.971	1.701	2	.029	8.706	1.795
89	1	1	.896	1	.828	.017	2	.172	3.158	.621
89	1	1	.896	1	.828	.017	2	.172	3.158	.621
90	1	1	.984	1	.800	.000	2	.200	2.777	.511
90	1	1	.984	1	.800	.000	2	.200	2.777	.511
91	1	1	.837	1	.845	.042	2	.155	3.431	.697
91	1	1	.837	1	.845	.042	2	.155	3.431	.697
92	1	1	.193	1	.971	1.694	2	.029	8.689	1.792
92	1	1	.193	1	.971	1.694	2	.029	8.689	1.792
93	1	2	.244	1	.963	1.355	1	.037	7.897	-2.320
93	1	2	.244	1	.963	1.355	1	.037	7.897	-2.320
94	1	1	.587	1	.905	.296	2	.095	4.796	1.034
94	1	1	.587	1	.905	.296	2	.095	4.796	1.034
95	1	2	.453	1	.530	.564	1	.470	.801	-.405
95	1	2	.453	1	.530	.564	1	.470	.801	-.405
96	2	2	.560	1	.910	.339	1	.090	4.967	-1.738
96	2	2	.560	1	.910	.339	1	.090	4.967	-1.738
97	1	1	.502	1	.921	.450	2	.079	5.368	1.161
97	1	1	.502	1	.921	.450	2	.079	5.368	1.161
98	1	1	.809	1	.852	.058	2	.148	3.562	.732
98	1	1	.809	1	.852	.058	2	.148	3.562	.732
99	1	1	.081	1	.986	3.052	2	.014	11.514	2.237
99	1	1	.081	1	.986	3.052	2	.014	11.514	2.237
100	1	1	.295	1	.956	1.099	2	.044	7.260	1.539
100	1	1	.295	1	.956	1.099	2	.044	7.260	1.539
101	1	1	.491	1	.555	.475	2	.445	.915	-.199
101	1	1	.491	1	.555	.475	2	.445	.915	-.199
102	1	1	.113	1	.981	2.509	2	.019	10.434	2.074
102	1	1	.113	1	.981	2.509	2	.019	10.434	2.074
103	1	2	.460	1	.535	.546	1	.465	.823	-.417
103	1	2	.460	1	.535	.546	1	.465	.823	-.417
104	2	2	.312	1	.953	1.020	1	.047	7.056	-2.166

105	1	1	.799	1	.718	.065	2	.282	1.937	.236
106	2	2	.870	1	.835	.027	1	.165	3.275	-1.319
106	2	2	.870	1	.835	.027	1	.165	3.275	-1.319
107	1	1	.798	1	.855	.065	2	.145	3.616	.746
107	1	1	.798	1	.855	.065	2	.145	3.616	.746
108	1	1	.002	1	.998	9.153	2	.002	21.825	3.516
108	1	1	.002	1	.998	9.153	2	.002	21.825	3.516
109	2	2	.193	1	.971	1.695	1	.029	8.693	-2.458
109	2	2	.193	1	.971	1.695	1	.029	8.693	-2.458
110	1	1	.975	1	.786	.001	2	.214	2.607	.459
110	1	1	.975	1	.786	.001	2	.214	2.607	.459
111	2	2	.750	1	.868	.101	1	.132	3.860	-1.474
111	2	2	.750	1	.868	.101	1	.132	3.860	-1.474
112	2	1	.960	1	.808	.003	2	.192	2.878	.541
112	2	1	.960	1	.808	.003	2	.192	2.878	.541
113	1	1	.783	1	.859	.076	2	.141	3.690	.765
113	1	1	.783	1	.859	.076	2	.141	3.690	.765
114	2	2	.604	1	.623	.268	1	.377	1.273	-.638
114	2	2	.604	1	.623	.268	1	.377	1.273	-.638
115	2	2	.850	1	.740	.036	1	.260	2.124	-.967
115	2	2	.850	1	.740	.036	1	.260	2.124	-.967
116	1	1	.933	1	.817	.007	2	.183	2.993	.574
116	1	1	.933	1	.817	.007	2	.183	2.993	.574
117	1	1	.632	1	.895	.230	2	.105	4.518	.970
117	1	1	.632	1	.895	.230	2	.105	4.518	.970
118	1	1	.485	1	.551	.489	2	.449	.897	-.209
118	1	1	.485	1	.551	.489	2	.449	.897	-.209
119	2	1	.583	1	.611	.302	2	.389	1.203	-.059
119	2	1	.583	1	.611	.302	2	.389	1.203	-.059
120	1	2	.911	1	.823	.012	1	.177	3.090	-1.267
120	1	2	.911	1	.823	.012	1	.177	3.090	-1.267
121	2	1	.994	1	.793	.000	2	.207	2.686	.483
121	2	1	.994	1	.793	.000	2	.207	2.686	.483
122	2	2	.987	1	.791	.000	1	.209	2.657	-1.140
122	2	2	.987	1	.791	.000	1	.209	2.657	-1.140
123	2	2	.671	1	.886	.180	1	.114	4.289	-1.581
123	2	2	.671	1	.886	.180	1	.114	4.289	-1.581
124	1	1	.854	1	.741	.034	2	.259	2.138	.306
124	1	1	.854	1	.741	.034	2	.259	2.138	.306
125	1	1	.489	1	.924	.480	2	.076	5.470	1.183
125	1	1	.489	1	.924	.480	2	.076	5.470	1.183
126	1	1	.962	1	.782	.002	2	.218	2.557	.443
126	1	1	.962	1	.782	.002	2	.218	2.557	.443
127	1	1	.854	1	.741	.034	2	.259	2.138	.306
127	1	1	.854	1	.741	.034	2	.259	2.138	.306
128	1	1	.294	1	.956	1.101	2	.044	7.266	1.540
128	1	1	.294	1	.956	1.101	2	.044	7.266	1.540
129	1	1	.963	1	.782	.002	2	.218	2.559	.444
129	1	1	.963	1	.782	.002	2	.218	2.559	.444
130	1	1	.468	1	.928	.526	2	.072	5.624	1.216
130	1	1	.468	1	.928	.526	2	.072	5.624	1.216
131	1	1	.680	1	.884	.170	2	.116	4.240	.903
131	1	1	.680	1	.884	.170	2	.116	4.240	.903
132	1	1	.828	1	.847	.047	2	.153	3.475	.708
132	1	1	.828	1	.847	.047	2	.153	3.475	.708
133	1	1	.748	1	.696	.103	2	.304	1.756	.169
133	1	1	.748	1	.696	.103	2	.304	1.756	.169
134	1	2	.434	1	.517	.613	1	.483	.746	-.373
134	1	2	.434	1	.517	.613	1	.483	.746	-.373
135	1	1	.738	1	.870	.112	2	.130	3.922	.824

136	1	1	.545	1	.589	.367	2	.411	1.083	-.115
137	2	2	.473	1	.544	.514	1	.456	.863	-.439
137	2	2	.473	1	.544	.514	1	.456	.863	-.439
138	1	2	.532	1	.581	.390	1	.419	1.044	-.531
138	1	2	.532	1	.581	.390	1	.419	1.044	-.531
139	2	2	.630	1	.637	.232	1	.363	1.355	-.674
139	2	2	.630	1	.637	.232	1	.363	1.355	-.674
140	1	2	.498	1	.560	.459	1	.440	.939	-.479
140	1	2	.498	1	.560	.459	1	.440	.939	-.479
141	1	2	.900	1	.826	.016	1	.174	3.138	-1.281
141	1	2	.900	1	.826	.016	1	.174	3.138	-1.281

** Misclassified case

Classification Results

			Predicted Group Membership		Total
		SEX	1.00	2.00	
		SEX	1.00	2.00	
Original	Count	1.00	79	20	99
Original	Count	1.00	79	20	99
		2.00	10	32	42
		2.00	10	32	42
	%	1.00	79.8	20.2	100.0
	%	1.00	79.8	20.2	100.0
		2.00	23.8	76.2	100.0
		2.00	23.8	76.2	100.0

a 78.7% of original grouped cases correctly classified.

Appendix 4 Discriminant function analysis with carapace as a coefficient.

Tests of Equality of Group Means

	Wilks' Lambda	F	df1	df2	Sig.
LH	.891	17.046	1	139	.000
LH	.891	17.046	1	139	.000
HFF	.772	41.016	1	139	.000
HFF	.772	41.016	1	139	.000
WH	.768	41.883	1	139	.000
WH	.768	41.883	1	139	.000
FOURTH	.810	32.710	1	139	.000
FOURTH	.810	32.710	1	139	.000
FIFTH	.769	41.853	1	139	.000
FIFTH	.769	41.853	1	139	.000
CW	.999	.082	1	139	.775
CW	.999	.082	1	139	.775

Stepwise Statistics

Wilks' Lambda

Step	Number of Variables	Lambda	df1	df2	df3	Exact F			
						Statistic	df1	df2	
Step						Statistic	df1	df2	
1	1	.768	1	1	139	41.883	1	139.000	1.531
1	1	.768	1	1	139	41.883	1	139.000	1.531
2	2	.662	2	1	139	35.194	2	138.000	4.414
2	2	.662	2	1	139	35.194	2	138.000	4.414
3	3	.635	3	1	139	26.257	3	137.000	1.622
3	3	.635	3	1	139	26.257	3	137.000	1.622
4	4	.602	4	1	139	22.463	4	136.000	2.043
4	4	.602	4	1	139	22.463	4	136.000	2.043
5	5	.583	5	1	139	19.350	5	135.000	2.187
5	5	.583	5	1	139	19.350	5	135.000	2.187

Summary of Canonical Discriminant Functions

Eigenvalues

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	.717	100.0	100.0	.646
1	.717	100.0	100.0	.646

a First 1 canonical discriminant functions were used in the analysis.

Wilks' Lambda

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1	.583	73.761	5	.000
1	.583	73.761	5	.000

Structure Matrix

	Function
	1
	1
WH	.648
WH	.648

FIFTH	.648
HFF	.642
HFF	.642
FOURTH	.573
FOURTH	.573
LH	.383
LH	.383
CW	.029
CW	.029

Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions Variables ordered by absolute size of correlation within function.

a This variable not used in the analysis.

Classification Statistics

Classification Function Coefficients

	SEX	
	1.00	2.00
	1.00	2.00
HFF	174.127	165.672
HFF	174.127	165.672
WH	316.832	281.804
WH	316.832	281.804
FOURTH	18.549	9.704
FOURTH	18.549	9.704
FIFTH	27.827	20.670
FIFTH	27.827	20.670
CW	212.765	224.781
CW	212.765	224.781
(Constant)	-394.561	-364.136
(Constant)	-394.561	-364.136

Fisher's linear discriminant functions

Casewise Statistics

		Actual Group	Highest Group				Second Highest Group			Discriminant Scores
			Predicted Group	P(D>d | G=g)	P(G=g | D=d)	Squared Mahalanobis Distance to Centroid	Group	P(G=g | D=d)	Squared Mahalanobis Distance to Centroid	Function 1
	Case Number		Predicted Group	P(D>d | G=g)	P(G=g | D=d)	Squared Mahalanobis Distance to Centroid	Group	P(G=g | D=d)	Squared Mahalanobis Distance to Centroid	Function 1
				pdf						
	Case Number			pdf						
Original	1	1	1	.771	1 .760	.085	2	.240	2.391	.256
Original	1	1	1	.771	1 .760	.085	2	.240	2.391	.256
	2	2	2	.819	1 .781	.052	1	.219	2.591	-1.062
	2	2	2	.819	1 .781	.052	1	.219	2.591	-1.062

3	1	1	.793	1	.770	.069	2	.230	2.481	.285
4	2	2	.767	1	.759	.088	1	.241	2.378	-.995
4	2	2	.767	1	.759	.088	1	.241	2.378	-.995
5	2	2	.668	1	.711	.183	1	.289	1.987	-.862
5	2	2	.668	1	.711	.183	1	.289	1.987	-.862
6	2	2	.932	1	.822	.007	1	.178	3.074	-1.206
6	2	2	.932	1	.822	.007	1	.178	3.074	-1.206
7	2	2	.659	1	.707	.194	1	.293	1.951	-.849
7	2	2	.659	1	.707	.194	1	.293	1.951	-.849
8	2	2	.487	1	.602	.482	1	.398	1.308	-.596
8	2	2	.487	1	.602	.482	1	.398	1.308	-.596
9	1	1	.530	1	.945	.395	2	.055	6.084	1.176
9	1	1	.530	1	.945	.395	2	.055	6.084	1.176
10	1	1	.198	1	.983	1.657	2	.017	9.766	1.835
10	1	1	.198	1	.983	1.657	2	.017	9.766	1.835
11	1	1	.624	1	.688	.240	2	.312	1.817	.058
11	1	1	.624	1	.688	.240	2	.312	1.817	.058
12	1	1	.830	1	.785	.046	2	.215	2.636	.333
12	1	1	.830	1	.785	.046	2	.215	2.636	.333
13	2	2	.191	1	.984	1.707	1	.016	9.888	-2.597
13	2	2	.191	1	.984	1.707	1	.016	9.888	-2.597
14	1	1	.549	1	.942	.358	2	.058	5.937	1.146
14	1	1	.549	1	.942	.358	2	.058	5.937	1.146
15	1	1	.437	1	.565	.604	2	.435	1.126	-.229
15	1	1	.437	1	.565	.604	2	.435	1.126	-.229
16	1	1	.707	1	.915	.142	2	.085	4.903	.924
16	1	1	.707	1	.915	.142	2	.085	4.903	.924
17	1	1	.328	1	.970	.955	2	.030	7.925	1.525
17	1	1	.328	1	.970	.955	2	.030	7.925	1.525
18	1	1	.510	1	.948	.433	2	.052	6.231	1.206
18	1	1	.510	1	.948	.433	2	.052	6.231	1.206
19	2	1	.863	1	.798	.030	2	.202	2.775	.375
19	2	1	.863	1	.798	.030	2	.202	2.775	.375
20	1	1	.777	1	.763	.080	2	.237	2.419	.265
20	1	1	.777	1	.763	.080	2	.237	2.419	.265
21	1	1	.304	1	.973	1.056	2	.027	8.210	1.575
21	1	1	.304	1	.973	1.056	2	.027	8.210	1.575
22	1	2	.885	1	.806	.021	1	.194	2.868	-1.146
22	1	2	.885	1	.806	.021	1	.194	2.868	-1.146
23	1	1	.483	1	.598	.493	2	.402	1.290	-.155
23	1	1	.483	1	.598	.493	2	.402	1.290	-.155
24	1	1	.272	1	.976	1.205	2	.024	8.617	1.645
24	1	1	.272	1	.976	1.205	2	.024	8.617	1.645
25	1	1	.964	1	.855	.002	2	.145	3.545	.592
25	1	1	.964	1	.855	.002	2	.145	3.545	.592
26	1	1	.997	1	.843	.000	2	.157	3.364	.544
26	1	1	.997	1	.843	.000	2	.157	3.364	.544
27	1	1	.404	1	.539	.695	2	.461	1.009	-.286
27	1	1	.404	1	.539	.695	2	.461	1.009	-.286
28	1	1	.572	1	.939	.320	2	.061	5.778	1.113
28	1	1	.572	1	.939	.320	2	.061	5.778	1.113
29	1	1	.166	1	.986	1.919	2	.014	10.388	1.933
29	1	1	.166	1	.986	1.919	2	.014	10.388	1.933
30	1	1	.127	1	.989	2.323	2	.011	11.304	2.072
30	1	1	.127	1	.989	2.323	2	.011	11.304	2.072
31	1	2	.467	1	.587	.528	1	.413	1.235	-.564
31	1	2	.467	1	.587	.528	1	.413	1.235	-.564
32	1	1	.606	1	.933	.266	2	.067	5.539	1.063
32	1	1	.606	1	.933	.266	2	.067	5.539	1.063
33	2	2	.567	1	.939	.328	1	.061	5.813	-1.864

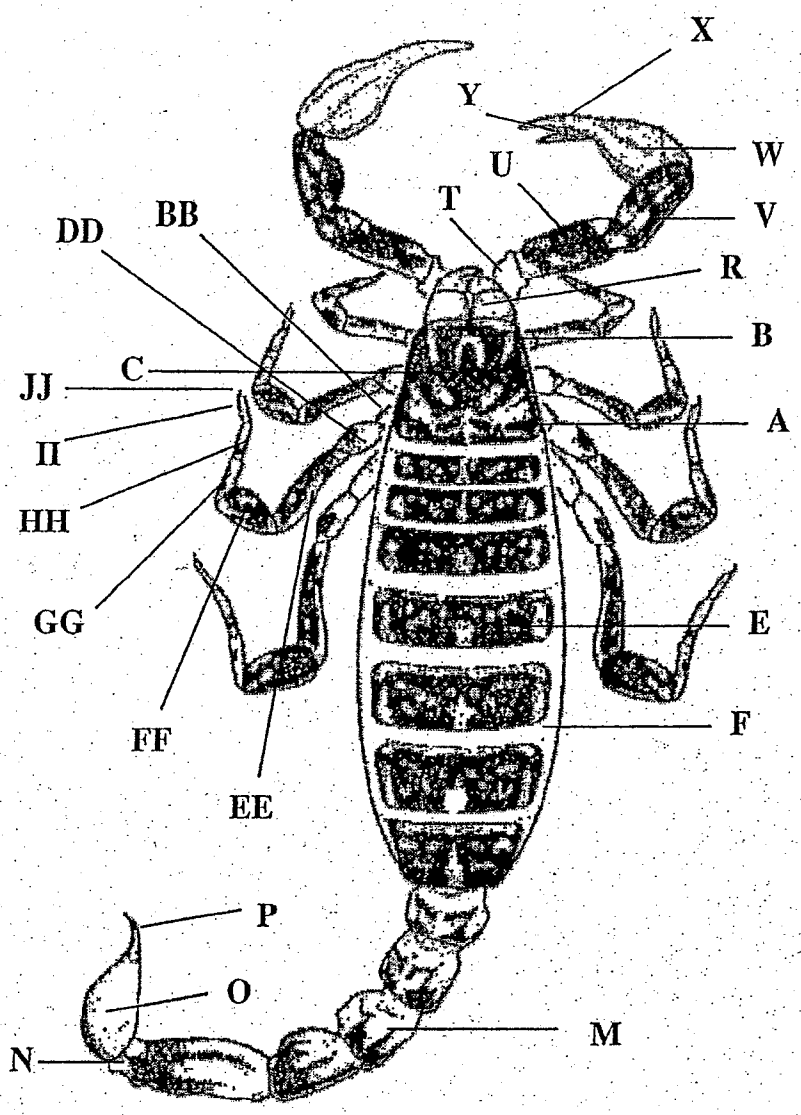
34	2	2	.671	1	.922	.180	1	.078	5.119	-1.715
35	2	2	.273	1	.976	1.204	1	.024	8.614	-2.388
35	2	2	.273	1	.976	1.204	1	.024	8.614	-2.388
36	2	2	.792	1	.769	.070	1	.231	2.478	-1.027
36	2	2	.792	1	.769	.070	1	.231	2.478	-1.027
37	1	1	.884	1	.805	.021	2	.195	2.863	.402
37	1	1	.884	1	.805	.021	2	.195	2.863	.402
38	2	2	.626	1	.689	.237	1	.311	1.825	-.804
38	2	2	.626	1	.689	.237	1	.311	1.825	-.804
39	1	1	.800	1	.773	.064	2	.227	2.511	.294
39	1	1	.800	1	.773	.064	2	.227	2.511	.294
40	1	1	.989	1	.848	.000	2	.152	3.431	.562
40	1	1	.989	1	.848	.000	2	.152	3.431	.562
41	1	1	.874	1	.802	.025	2	.198	2.822	.389
41	1	1	.874	1	.802	.025	2	.198	2.822	.389
42	2	2	.149	1	.987	2.078	1	.013	10.754	-2.732
42	2	2	.149	1	.987	2.078	1	.013	10.754	-2.732
43	2	2	.642	1	.927	.216	1	.073	5.300	-1.755
43	2	2	.642	1	.927	.216	1	.073	5.300	-1.755
44	2	2	.779	1	.901	.078	1	.099	4.486	-1.571
44	2	2	.779	1	.901	.078	1	.099	4.486	-1.571
45	1	1	.960	1	.856	.003	2	.144	3.566	.598
45	1	1	.960	1	.856	.003	2	.144	3.566	.598
46	2	2	.911	1	.869	.012	1	.131	3.800	-1.402
46	2	2	.911	1	.869	.012	1	.131	3.800	-1.402
47	1	2	.416	1	.960	.661	1	.040	7.029	-2.104
47	1	2	.416	1	.960	.661	1	.040	7.029	-2.104
48	2	1	.788	1	.768	.072	2	.232	2.462	.279
48	2	1	.788	1	.768	.072	2	.232	2.462	.279
49	2	2	.745	1	.908	.106	1	.092	4.679	-1.616
49	2	2	.745	1	.908	.106	1	.092	4.679	-1.616
50	1	1	.298	1	.973	1.084	2	.027	8.290	1.589
50	1	1	.298	1	.973	1.084	2	.027	8.290	1.589
51	1	1	.530	1	.945	.394	2	.055	6.079	1.175
51	1	1	.530	1	.945	.394	2	.055	6.079	1.175
52	1	2	.363	1	.504	.827	1	.496	.862	-.381
52	1	2	.363	1	.504	.827	1	.496	.862	-.381
53	1	1	.768	1	.903	.087	2	.097	4.548	.842
53	1	1	.768	1	.903	.087	2	.097	4.548	.842
54	2	2	.239	1	.979	1.384	1	.021	9.086	-2.467
54	2	2	.239	1	.979	1.384	1	.021	9.086	-2.467
55	1	2	.721	1	.737	.128	1	.263	2.191	-.933
55	1	2	.721	1	.737	.128	1	.263	2.191	-.933
56	1	2	.862	1	.797	.030	1	.203	2.769	-1.117
56	1	2	.862	1	.797	.030	1	.203	2.769	-1.117
57	2	2	.015	1	.998	5.956	1	.002	18.305	-3.731
57	2	2	.015	1	.998	5.956	1	.002	18.305	-3.731
58	1	1	.413	1	.961	.669	2	.039	7.054	1.365
58	1	1	.413	1	.961	.669	2	.039	7.054	1.365
59	2	2	.418	1	.550	.655	1	.450	1.058	-.481
59	2	2	.418	1	.550	.655	1	.450	1.058	-.481
60	2	2	.530	1	.631	.394	1	.369	1.464	-.663
60	2	2	.530	1	.631	.394	1	.369	1.464	-.663
61	1	1	.705	1	.916	.144	2	.084	4.915	.926
61	1	1	.705	1	.916	.144	2	.084	4.915	.926
62	1	1	.593	1	.670	.285	2	.330	1.700	.013
62	1	1	.593	1	.670	.285	2	.330	1.700	.013
63	1	1	.022	1	.997	5.281	2	.003	17.107	2.846
63	1	1	.022	1	.997	5.281	2	.003	17.107	2.846
64	1	1	.678	1	.921	.173	2	.079	5.079	.963

96	2	2	.791	1	.898	.071	1	.102	4.425	-1.556
97	1	1	.382	1	.964	.764	2	.036	7.354	1.421
97	1	1	.382	1	.964	.764	2	.036	7.354	1.421
98	1	1	.913	1	.869	.012	2	.131	3.789	.656
98	1	1	.913	1	.869	.012	2	.131	3.789	.656
99	1	1	.122	1	.989	2.386	2	.011	11.442	2.092
99	1	1	.122	1	.989	2.386	2	.011	11.442	2.092
100	1	1	.448	1	.956	.575	2	.044	6.741	1.306
100	1	1	.448	1	.956	.575	2	.044	6.741	1.306
101	1	1	.360	1	.502	.838	2	.498	.851	-.368
101	1	1	.360	1	.502	.838	2	.498	.851	-.368
102	1	1	.148	1	.987	2.097	2	.013	10.797	1.995
102	1	1	.148	1	.987	2.097	2	.013	10.797	1.995
103	1	1	.649	1	.701	.207	2	.299	1.912	.092
103	1	1	.649	1	.701	.207	2	.299	1.912	.092
104	2	1	.435	1	.563	.609	2	.437	1.118	-.233
104	2	1	.435	1	.563	.609	2	.437	1.118	-.233
105	1	1	.634	1	.929	.227	2	.071	5.355	1.024
105	1	1	.634	1	.929	.227	2	.071	5.355	1.024
106	2	2	.508	1	.948	.437	1	.052	6.246	-1.952
106	2	2	.508	1	.948	.437	1	.052	6.246	-1.952
107	1	1	.795	1	.897	.067	2	.103	4.399	.807
107	1	1	.795	1	.897	.067	2	.103	4.399	.807
108	1	1	.003	1	.999	8.612	2	.001	22.778	3.482
108	1	1	.003	1	.999	8.612	2	.001	22.778	3.482
109	2	2	.184	1	.984	1.761	1	.016	10.017	-2.618
109	2	2	.184	1	.984	1.761	1	.016	10.017	-2.618
110	1	1	.983	1	.839	.000	2	.161	3.299	.526
110	1	1	.983	1	.839	.000	2	.161	3.299	.526
111	2	2	.999	1	.844	.000	1	.156	3.373	-1.289
111	2	2	.999	1	.844	.000	1	.156	3.373	-1.289
112	2	1	.854	1	.794	.034	2	.206	2.735	.363
112	2	1	.854	1	.794	.034	2	.206	2.735	.363
113	1	1	.260	1	.977	1.267	2	.023	8.784	1.673
113	1	1	.260	1	.977	1.267	2	.023	8.784	1.673
114	2	2	.546	1	.641	.365	1	.359	1.523	-.687
114	2	2	.546	1	.641	.365	1	.359	1.523	-.687
115	2	2	.884	1	.805	.021	1	.195	2.861	-1.144
115	2	2	.884	1	.805	.021	1	.195	2.861	-1.144
116	1	1	.622	1	.931	.243	2	.069	5.433	1.041
116	1	1	.622	1	.931	.243	2	.069	5.433	1.041
117	1	1	.502	1	.949	.451	2	.051	6.296	1.219
117	1	1	.502	1	.949	.451	2	.051	6.296	1.219
118	1	2	.397	1	.533	.716	1	.467	.984	-.444
118	1	2	.397	1	.533	.716	1	.467	.984	-.444
119	2	2	.385	1	.523	.755	1	.477	.939	-.422
119	2	2	.385	1	.523	.755	1	.477	.939	-.422
120	1	2	.945	1	.827	.005	1	.173	3.129	-1.221
120	1	2	.945	1	.827	.005	1	.173	3.129	-1.221
121	2	1	.962	1	.832	.002	2	.168	3.204	.500
121	2	1	.962	1	.832	.002	2	.168	3.204	.500
122	2	2	.891	1	.875	.019	1	.125	3.903	-1.428
122	2	2	.891	1	.875	.019	1	.125	3.903	-1.428
123	2	2	.904	1	.871	.015	1	.129	3.837	-1.411
123	2	2	.904	1	.871	.015	1	.129	3.837	-1.411
124	1	1	.972	1	.835	.001	2	.165	3.251	.513
124	1	1	.972	1	.835	.001	2	.165	3.251	.513
125	1	1	.389	1	.964	.743	2	.036	7.290	1.409
125	1	1	.389	1	.964	.743	2	.036	7.290	1.409
126	1	1	.801	1	.773	.064	2	.227	2.513	.295

127	1	1	.875	1	.879	.025	2	.121	3.982	.705
128	1	1	.453	1	.956	.562	2	.044	6.696	1.297
128	1	1	.453	1	.956	.562	2	.044	6.696	1.297
129	1	1	.939	1	.862	.006	2	.138	3.665	.624
129	1	1	.939	1	.862	.006	2	.138	3.665	.624
130	1	1	.520	1	.946	.413	2	.054	6.153	1.190
130	1	1	.520	1	.946	.413	2	.054	6.153	1.190
131	1	1	.483	1	.952	.491	2	.048	6.445	1.248
131	1	1	.483	1	.952	.491	2	.048	6.445	1.248
132	1	1	.907	1	.814	.014	2	.186	2.961	.430
132	1	1	.907	1	.814	.014	2	.186	2.961	.430
133	1	1	.849	1	.792	.036	2	.208	2.713	.357
133	1	1	.849	1	.792	.036	2	.208	2.713	.357
134	1	1	.510	1	.617	.434	2	.383	1.389	-.112
134	1	1	.510	1	.617	.434	2	.383	1.389	-.112
135	1	1	.358	1	.967	.845	2	.033	7.601	1.467
135	1	1	.358	1	.967	.845	2	.033	7.601	1.467
136	1	1	.943	1	.826	.005	2	.174	3.121	.476
136	1	1	.943	1	.826	.005	2	.174	3.121	.476
137	2	2	.795	1	.771	.067	1	.229	2.492	-1.031
137	2	2	.795	1	.771	.067	1	.229	2.492	-1.031
138	1	1	.393	1	.963	.731	2	.037	7.251	1.402
138	1	1	.393	1	.963	.731	2	.037	7.251	1.402
139	2	2	.985	1	.839	.000	1	.161	3.309	-1.272
139	2	2	.985	1	.839	.000	1	.161	3.309	-1.272
140	1	1	.449	1	.574	.573	2	.426	1.169	-.209
140	1	1	.449	1	.574	.573	2	.426	1.169	-.209
141	1	2	.783	1	.765	.076	1	.235	2.440	-1.015
141	1	2	.783	1	.765	.076	1	.235	2.440	-1.015

** Misclassified case

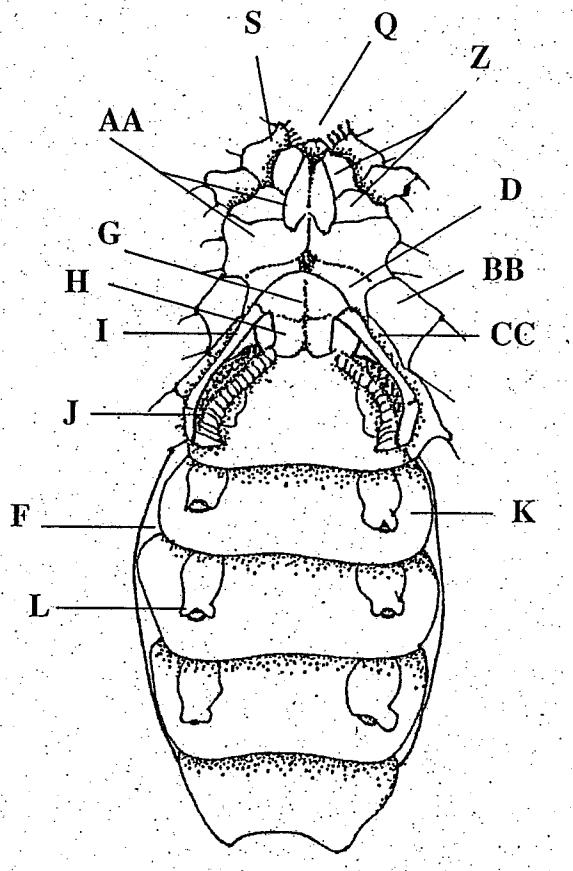
Morphology of *Cercophonius squama*



Prosoma:
A. Carapace
B. Lateral Eyes
C. Median Eyes
D. Sternum

Opisthosoma
Mesosoma:
E. Tergite of 4th mesosomal segment
F. Pleural Membrane
G. Genital Operculum
H. Basal Piece of Pectines
I. Pectine
J. Pectinal Teeth
K.Sternite of 4th mesosomal segment
L. Spiracle of Book Lung

Metasoma:
M. 3rd metasomal segment
N. Anus
O. Vesiscle of Telson
P. Aculeus of Telson



Appendages:

Q. Preoral Chamber
R. Chelicera
S. Coxa of Pedipalp
T. Trochanter of Pedipalp
U. Femur of Pedipalp
V. Patella of Pedipalp
W. Chela Manus of Pedipalp
X. Fixed Finger of Pedipalp Chela
Y. Movable Finger of Pedipalp Chela
Z. Coxa of Leg 1
AA. Coxa of Leg 2
BB. Coxa of Leg 3
CC. Coxa of Leg 4
DD. Trochanter of Leg 3
EE. Femur of Leg 3
FF. Patella of Leg 3
GG. Tibia of Leg 3
HH. Basitarsus of Leg 3
II. Tarsus of Leg 3
JJ. Tarsal Claw